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Abstract—Otolith thermal marking is an efficient method for mass marking hatchery-reared salmon and can be used to estimate the proportion of hatchery fish captured in a mixed-stock fishery. Accuracy of the thermal pattern classification depends on the prominence of the pattern, the methods used to prepare and view the patterns, and the training and experience of the personnel who determine the presence or absence of a particular pattern. Estimating accuracy rates is problematic when no secondary marking is available and no error-free standards exist. Agreement measures, such as *kappa* (κ), provide a relative measure of the reliability of the determinations when independent readings by two readers are available, but the magnitude of κ can be influenced by the proportion of marked fish. If a third reader is used or if two or more groups of paired readings are examined, latent class models can provide estimates of the error rates of each reader. Applications of κ and latent class models are illustrated by a program providing contribution estimates of hatchery-reared chum and sockeye salmon in Southeast Alaska.

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The use of agreement measures and latent class models to assess the reliability of classifying thermally marked otoliths*

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The ability to induce patterns in salmon otoliths by manipulating water temperatures has proved to be an efficient means for marking large numbers of salmon (Volk et al., 1990). When salmon embryos or alevins are exposed to a rapid drop in temperature, otolith growth is temporarily disrupted, and this results in a discontinuity in the otolith's microstructure. When viewed under transmitted light microscopy, this discontinuity appears as a dark ring. By controlling the number of temperature drops and the timing between drops, a coded pattern of dark rings can be recorded on the otolith and this pattern can be recovered from otoliths of older fish by removing the overlaying material and exposing the otolith core. For hatcheries that release a large number of fish, this type of marking method has shown to be particularly cost effective for marking 100% of the releases (Munk et al., 1993).

Several fisheries management programs in Alaska use thermal marking to estimate hatchery contributions to commercial fisheries (Hagen et al., 1995). Typically, several hundred salmon otoliths are systematically collected during each two- or three-day commercial opening during the fishing season. The otoliths and sampling data are shipped to a processing laboratory where a subsample of otoliths (generally 50 to 100) are processed immediately to meet in-season management needs; a portion of the remaining otoliths are processed later to provide an overall estimate of hatchery contribution to the fisheries.

The process by which a reader determines the presence or absence of a thermal mark in an otolith can be characterized as one of pattern recognition and image matching. Prior to examining otoliths of unknown origin, the readers gain familiarity with the patterns likely to be encountered by carefully examining fry otoliths that were obtained after thermal marking but prior to their release into the wild. Because there can be wide variation in the appearance of the thermal marks within a mark group (due in part to differences in developmental stages at marking), a single mark group may be represented by a variety of patterns. As a result, secondary characteristics and measurements of the patterns are sometimes necessary to identify an otolith to a mark group. The examination is also used to confirm that all the hatchery fish have been successfully marked.

The process of making a determination on otoliths from returning adult salmon can become problematic because wild salmon may also contain otolith patterns that can mimic the features imposed through thermal marking. Referred to as "noisy patterns," their presence can increase the rate of false positives. Conversely, if the hatchery employs poor temperature control or unintended disruptions occur around the period of marking, it may be difficult to identify the otolith as that of a

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hatchery fish, and this would increase the rate of false negatives. Differences between readers in skill and training level, and how they process otoliths, can add to the uncertainty in estimating the accuracy of the readings and the rates of false positives and negatives.

Otolith marking generally takes place without any secondary marking, such as fin-clipping or coded-wire-tagging; therefore the accuracy of a reading cannot directly be determined through conventional methods that make use of a "gold standard" (known origin sample) or other error-free classification methods. To ensure that the information provided to the Alaskan fisheries managers is accurate, each otolith is independently examined by two readers, and a third reading is used to resolve differences between the first two readings. The resolved readings are used to estimate the contribution of hatchery fish, and the presumption of accuracy is based on the premise that, through multiple readings, all marked fish are either correctly identified or that errors, if present, are inconsequential. Developing the analytical tools to determine the veracity of that assumption is the objective of this investigation, and by establishing such tools, quality control standards for recovering thermal marks can be developed.

In developing the tools to measure the quality of otolith readings, three questions are addressed:

1 How to assess the reliability of otolith readings when no standards are available.
2 How to estimate the proportion of hatchery marks when there is disagreement between two or more readers.
3 How the precision of the estimate of the proportion is influenced by classification error.

We discuss two approaches: 1) indices of agreement typically used in reliability studies, and 2) latent class models where classification errors are estimated for each reader even though the true error rate is considered unknown. The data requirements and their attendant assumptions are presented for each approach. The methods are illustrated by examining among-reader comparisons of chum salmon (*Oncorhynchus keta*) and sockeye (*Oncorhynchus nerka*) salmon otoliths collected from programs that monitor inseason contributions of hatchery fish in several commercial fisheries in Southeast Alaska (Hagen et al., 1995). The results are used to provide recommendations for monitoring the quality of otolith readings for thermal marking programs.

Methods

Standard available

A sample of n otoliths, which are examined by two readers, can be cross-classified as hatchery (H) or wild stock (W) as in Table 1. Suppose we wish to estimate the accuracy rate (probability of making a correct classification) or conversely, the error rate (probability of making a wrong classification). If we know nothing about reader 1, but reader 2 is infallible (or is considered a "gold standard"), unbiased estimates of the accuracy and error rates of reader 1 and the proportion of hatchery stocks (p) are given by

$$\hat{\pi}^{(1)}_{\mathrm{H|H}} = n_{\mathrm{HH}}/n_{\mathrm{H}}, \qquad \hat{\pi}^{(1)}_{\mathrm{W|H}} = n_{\mathrm{WH}}/n_{\mathrm{H}} = 1-\hat{\pi}_{\mathrm{H|H}}$$

$$\hat{\pi}^{(1)}_{\mathrm{W|W}} = n_{\mathrm{WW}}/n_{\mathrm{W}}, \qquad \hat{\pi}^{(1)}_{\mathrm{H|W}} = n_{\mathrm{HW}}/n_{\mathrm{W}} = 1-\hat{\pi}_{\mathrm{W|W}}$$

$$\hat{p} = n_{\mathrm{H}}/n,$$

(where, for example, $\pi^{(1)}_{\mathrm{W|H}}$ refers to the probability that reader 1 classifies an otolith as W when its true state is H). These estimates reflect the fact that reader 2 is infallible; the accuracy rates ($\hat{\pi}_{\mathrm{H|H}}$, $\hat{\pi}_{\mathrm{W|W}}$) and the error rates ($\hat{\pi}_{\mathrm{W|H}}$, $\hat{\pi}_{\mathrm{H|W}}$) are conditional on the numbers of hatchery or wild stock otoliths as determined by reader 2.

Table 1

Notation used to show the cross-classification of a sample of n otoliths by two readers to either hatchery (H) or wild stock (W) assignment. Row and column sums are indicated by the subscript "·".

		Reader 2		
		H	W	
Reader 1	H	n_{HH}	n_{HH}	$n_{\mathrm{H}\cdot}$
	W	n_{WH}	n_{WW}	$n_{\mathrm{W}\cdot}$
		$n_{\cdot\mathrm{H}}$	$n_{\cdot\mathrm{W}}$	n

No standard available

If a standard is not available, an unbiased estimate of p can be obtained if the accuracy rates for reader 1 are known. The estimate is

$$\hat{p}^{*} = (n_{\mathrm{H}}/n + \pi^{(1)}_{\mathrm{W|W}} - 1)/(\pi^{(1)}_{\mathrm{H|H}} + \pi^{(1)}_{\mathrm{W|W}} - 1),$$

where n_{H} is the number of otoliths classified as hatchery otoliths. If the accuracy rates are estimated, then $\hat{p}^{*}$ will no longer be unbiased, but will be much less biased than the estimator n_{H}/n and will in general have a much smaller mean-squared error (Rogan and Gladen, 1978). For a Bayesian approach to this problem, see Viana et al. (1993) and Joseph et al. (1995).

Agreement measures When accuracy rates are unavailable, statistics that measure "agreement" between readers are often calculated (e.g. Fleiss, 1981). One such index is simply the proportion of observed agreement (P_o), defined as

$$P_o = (n_{\mathrm{HH}} + n_{\mathrm{WW}})/n.$$

Another index, called *kappa* (κ), corrects P_o for the degree of agreement that is expected by chance alone. It is defined as

$$\kappa = (P_o - P_e)/(1 - P_e),$$

where P_e = expected agreement = $(n_{H}n_{\cdot H} + n_{W}n_{W})/n^2$. The divisor, $1 - P_e$, constrains κ to be less than or equal to one, and if all agreement is due to chance (P_o=P_e), then κ equals zero. Note that with κ, independence between readers is assumed in order to calculate expected agreement.

An example of how agreement indices can be used to monitor readings is shown in Figure 1, which displays κ and its standard error for 2874 chum otoliths readings divided into 27 groups based on different reader pairs and capture locations. Included are P_o's for four of the groups. The results indicate that κ levels were similar between the different groups, suggesting overall consistency in readings, although some of the groups had lower values, which in practice would invite further investigation.

The P_o's in Figure 1 have a different rank order than the κ values. This apparent discrepancy highlights a potential problem in interpretation when using agreement indices to draw conclusions. To help illustrate this point, consider the following examples (Table 2). Table 2A is generated as the expected counts, given $\pi_{H|H} = 0.9$ and $\pi_{W|W} = 1.0$ for both readers, and $p = 0.1$. In this case, $P_o = 0.98$ and $\kappa = 0.89$. On the other hand, Table 2B is generated under the same assumptions except that $\pi_{H|H} = 0.5$. In this case P_o drops only slightly to 0.95, whereas κ drops to 0.47. Because the hatchery stock is rare, the inability of the readers to detect the mark is not well reflected by P_o, whereas κ reflects it better by correcting for the high level of chance agreement.

Now let $\pi_{H|H} = 0.9$ and $\pi_{W|W} = 0.9$ for both readers, and P= 0.5 (Table 2C). In this case, $P_o = 0.82$ and $\kappa = 0.64$. On the other hand, Table 2D is generated under the same assumptions except that P= 0.05. In this case, P_o remains unchanged at 0.82, but κ drops to 0.25.

In none of the above examples is the index "wrong." Rather, as is the case with most indices, interpretation is affected by the values of the underlying parameters. In the latter example (Table 2, C–D), even though P_o is the same for C and D, the scale it is being compared with has changed, thus changing the value of κ. This increases the difficulty of comparing κ across populations with different underlying proportions. Note also that Table 2D could have been derived from $\pi_{H|H} = 0.5$ and $\pi_{W|W} = 0.944$ for both readers, and $p = 0.19$. Thus, without additional information, it is impossible to draw reliable conclusions about reader accuracies or the proportion of hatchery marks.

Although agreement measures can be ambiguously interpreted, in practice they can still serve a useful monitoring role during routine comparisons when the circumstances of the readings are fairly well characterized. The interpretive difficulties with indices such κ and P_o become apparent when trying to translate agreement measures into statements about the accuracy of different readers and about the influence of reading error on the contribution estimates.

Latent class models An alternative approach is to try to estimate $\pi_{H|H}$ and $\pi_{W|W}$ for each reader, along with p. Although at first thought this may seem impossible, it can

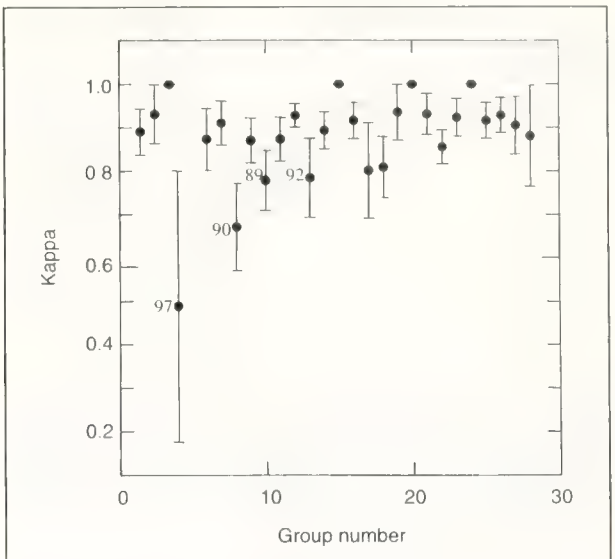

Figure 1

The values of κ (±1 SE) from 27 groups of paired readings of chum salmon otoliths (total=2874). The groups are based on pairs of different readers examining otoliths collected at different times and locations. The proportion of agreement (P_o) is shown next to group 4, 7, 9, and 12 for comparison with the value of κ.

be shown that either by setting a few constraints or by collecting additional information, estimation is indeed possible. This problem falls into the category of latent class modeling (e.g. Everitt, 1984; Bartholomew, 1987; McCutcheon, 1987; Clogg, 1995). Latent class models (LCMs) belong to a family of latent variable models that hypothesize the existence of unobservable "latent" variables, about which information can be obtained only though measurements on observable "manifest" variables. LCMs specifically restrict the latent and manifest variables to be categorical. In the present situation, the latent variable is the true class (H or W) to which the otolith belongs, whereas the manifest variables are the readers' classifications. Such models have been used for assessing reliability of diagnostic tests in the medical field over the last 20 years (see Walter and Irwig, 1988; Formann, 1996, for reviews).

Returning to the problem with two readers, neither of which is a standard, there are five essential parameters to estimate: $\pi^{(1)}_{H|H}, \pi^{(2)}_{H|H}, \pi^{(1)}_{W|W}, \pi^{(2)}_{W|W}$, and p, with only 3 df (four pieces of data, n_{HH}, n_{HW}, n_{WH}, n_{WW}, minus one because the sample size, n, is fixed). Thus, the model is overparameterized, and either constraints on the parameters or more data are needed. Possible constraints include 1) considering that two of the parameters are known (e.g. $\pi^{(1)}_{W|W} = \pi^{(2)}_{W|W} = 1$; i.e. both readers always call a wild stock correctly, there are no "false positives"), or 2) considering that two sets of parameters are equal (e.g. $\pi^{(1)}_{H|H}, \pi^{(2)}_{H|H}, \pi^{(1)}_{W|W} = \pi^{(2)}_{W|W}$; i.e. the accuracy rates are the same for both readers).

Although there may be times when such constraints are realistic, in general they will not be; therefore more infor-

mation will be necessary. One way to generate more information is to have a third independent reader (Walter, 1984). With three readers, there are seven essential parameters: $\pi_{H|H}^{(1),(2),(3)}$, $\pi_{W|W}^{(1),(2),(3)}$ and p. There is also $2^3 - 1 = 7$ df, so that all the parameters are estimable. Estimation is most commonly done by the method of maximum likelihood.

If readings are assumed to be independent among readers and among otoliths, the likelihood function is

$$\prod_{i} \prod_{H,W} \prod_{j} \prod_{H,W} \prod_{k} \prod_{H,W} \left\{ p\pi_{i|H}^{1} \pi_{j|H}^{2} \pi_{k|H}^{3} + (1-p)\pi_{i|W}^{1} \pi_{j|W}^{2} \pi_{k|W}^{3} \right\}^{n_{ijk}}.$$

This likelihood function must be maximized numerically and methods for this computation will be discussed later.

If more than three readers are used, there are extra degrees of freedom that can be used to assess goodness-of-fit. For example, with four readers there will be nine parameters with 15 df, leaving 6 df for goodness-of-fit. Pearson chi-square or likelihood ratio G^2 tests would both be applicable.

Another way to generate additional information was proposed by Hui and Walter (1980). Suppose there are two or more strata with different hatchery proportions in each strata. For example, catch could be stratified temporally or spatially. If it is assumed that $\pi_{H|H}^{(k)}$ and $\pi_{W|W}^{(k)}$ remain constant over strata, then a solution for just two readers may be obtained. For example, if there are two readers and two strata, then there are six parameters: $\pi_{H|H}^{(1),(2)}$, $\pi_{W|W}^{(1),(2)}$, p_1, and p_2, with $2(2^2 - 1) = 6$ df. Increasing the number of strata increases the degrees of freedom; e.g. three strata for two readers gives $3(2^2 - 1) = 9$ df for 7 parameters. The likelihood function for two readers and S strata is

$$\prod_{g=1}^{S} \prod_{i=H,W} \prod_{j} \prod_{H,W} \left\{ p_g \pi_{i|H}^{1} \pi_{j|H}^{2} + (1-p_g)\pi_{i|W}^{1} \pi_{j|W}^{2} \right\}^{n_{ij}}.$$

A third way to supply additional information is to take a Bayesian approach (see "Discussion" section). By specifying prior distributions of the model parameters, unique estimates can be obtained (Joseph et al., 1995).

A critical assumption in the above models is that readings are independent. Specifically, the reading of each otolith by a given reader is independent of any other reading by the same reader, and each reading by various readers on a given otolith is independent given the true state of the otolith. In principle, the latter assumption may be difficult to meet especially if all readers examine the same otolith. The fact that the otolith is not prepared independently by each reader could induce a dependence among the readers. Also, variability in the readability of the mark due to the marking process can induce a dependence. Such dependence can bias the estimators of π and p (Vacek, 1985). Note that this latter assumption of independence is also required for κ.

One remedy for the problem of dependence due to preparation is to require independent preparations. This however, requires additional otoliths and with only two otoliths per fish, this would limit the number of readers to two. But in practice, this may not be a large concern. Typically, the second reader has the option to provide additional processing effort to the first otolith or, if needed, to process the second otolith. In almost all cases additional preparation is not done and readers feel they are able to extract sufficient information about the presence or absence of a mark from each other's preparations. In addition, reader accuracy rates obtained by LCM do not appear to vary systematically with the reading order, which also suggests that preparation-induced dependency is not a significant factor.

Dependency associated with variability in the appearance of the mark may be harder to address. A general solution is to model the dependence with additional parameters (e.g. Vacek, 1985; Qu et al., 1996; Yang and Becker, 1997; Qu and Hagdu; 1998; Albert et al., 2001). Modeling dependence requires either more readers or more strata. These modeling approaches are complicated and are currently evolving (see Albert et al., 2001). Alternatively, ad-

Table 2

Examples from cross-classification data generated as expected counts from a sample of 1000 otoliths based on different accuracy rates for identifying hatchery fish ($\pi_{H|H}$) and wild fish ($\pi_{W|W}$) under different mark proportions (p). The examples used illustrate differences between observed agreement (P_o) and chance-corrected agreement (κ) under different underlying conditions.

		Reader 2				
A		H	W			
Reader 1	H	81	9	90	$\pi_{H\|H} = 0.9$	$P_o = 0.98$
	W	9	901	910	$\pi_{W\|W} = 1.0$	$\kappa = 0.89$
	Total	90	910	1000	$p = 0.1$	
B		Reader 2				
		H	W			
Reader 1	H	25	25	50	$\pi_{H\|H} = 0.5$	$P_o = 0.95$
	W	25	925	950	$\pi_{W\|W} = 1.0$	$\kappa = 0.47$
	Total	50	950	1000	$p = 0.1$	
C		Reader 2				
		H	W			
Reader 1	H	410	90	500	$\pi_{H\|H} = 0.9$	$P_o = 0.82$
	W	90	410	500	$\pi_{W\|W} = 0.9$	$\kappa = 0.64$
	Total	500	500	1000	$p = 0.5$	
D		Reader 2				
		H	W			
Reader 1	H	50	90	140	$\pi_{H\|H} = 0.9$	$P_o = 0.82$
	W	90	770	860	$\pi_{W\|W} = 0.9$	$\kappa = 0.25$
	Total	140	860	1000	$p = 0.05$	

ditional latent classes may be added (Christensen et al., 1992; Formann, 1994), e.g. a third class of otoliths from ambiguous sources.

In the previous discussion concerning three or more readers, we implied that readers were different individuals. This need not be so; what is required are three or more independent readings. If it were possible for the same individual to read the same otolith more than once, independently, then the number of different readers could be reduced. If independence could not be met, the dependence could be modeled, as discussed above.

Another critical assumption, but one that should be met most of the time, is that the individual accuracy rates are known to be either greater than or less than the error rates (e.g. $\pi_{H|H} > \pi_{W|H}$ and $\pi_{W|W} > \pi_{H|W}$, which implies that $\pi_{H|H}$ and $\pi_{W|W}$ are either greater than or less than 0.5) because of an inherent symmetry in the problem that results in the same likelihood function being generated when the error rates are switched with the accuracy rates.

Computation Formulas for estimating κ and its standard error are straightforward (Fleiss, 1981). Estimates can also be obtained from several software packages including PROC FREQ in SAS (SAS Institute, 1989).

Maximizing either of the likelihood functions for the LCMs requires a numerical procedure. The most straightforward is to use an optimization routine such as "Solver" in Excel (Microsoft Corporation, 1993) or "nlminb" in S-PLUS (Statistical Sciences, 1995). Alternatively, the EM algorithm (Dempster et al., 1977; Dawid and Skene, 1979; McLachlan and Krishnan, 1997) can be easily used. The simplicity of the EM algorithm follows from the recognition that the LCM is an example of a finite mixture problem, specifically, in this case, a mixture of multivariate Bernoulli distributions with mixing parameter p (Everitt, 1984). Use of the EM algorithm for such mixture problems in fisheries is well documented, e.g. for stock composition estimates (Millar, 1987; Pella et al., 1996) and for age-length keys (Kimura and Chikuni, 1987). A more efficient alternative to the EM algorithm is to use iteratively reweighted least squares (Agresti, 1990). This method is relatively easy to implement in software such as PROC NLIN in SAS (SAS Institute, 1989). Perhaps the most direct and efficient way would be to use LCM software. We are not aware of any routines for LCMs in any major statistical package at present, but several independent LCM packages exist (for a review, see Clogg, 1995; and for an Internet listing see http://ourworld.compuserve.com/homepages/jsuebersax/index.htm).

As with many maximum likelihood problems, where numerical methods must be used, complications can arise. Constraints may at times be needed to ensure that parameter estimates fall in acceptable intervals (e.g. [0,1] for p and [0.5,1] for the π's). Also the likelihood function may have local maxima, which means that several runs with varying starting values may be necessary to identify the global maximum. Finally, estimates of standard errors may entail additional computing. PROC NLIN in SAS provides asymptotic (i.e. large-sample) standard errors. Jackknife and bootstrap estimates are relatively easy to program, the jackknife being much less computationally intensive.

Finally, the Bayesian programs discussed in Joseph et al. (1995) can be found at http://www.epi.mcgill.ca/Joseph/software.html.

Examples

The first example analyzes the results of three readers examining 570 chum otoliths. The samples were taken from a common location, and the readers were familiar with the patterns. Each reading was made without knowledge of prior readings. The data, along with pairwise κ estimates and the LCM parameter estimates (using PROC NLIN in SAS; see appendix for code) are presented in Table 3.

These results indicate that the third reader is significantly (α=0.05) less able to correctly identify a hatchery mark when it is present and that there are no significant differences among readers in their ability to detect a wild mark when it is present. These conclusions are readily apparent from the table of results, and although the pairwise κ's are consistent with these results, they are more difficult to interpret. With the variance due to sampling estimated to be $(0.7379)(1 - 0.7379)/(570 - 1) = 0.0003399$, misclassification error contributes only 0.36% to the total variance.

The second example consists of two readers with four spatial strata. Samples were obtained from sockeye salmon caught in four neighboring Alaskan gillnet fisheries in central Southeast Alaska. The data and the LCM estimates are shown in Table 4. These estimates indicate that the readers are not statistically different in their ability to detect hatchery marks, whereas the second reader is better able to distinguish wild marks. With eight parameters and 12 df, there are 4 df available for a goodness-of-fit test. Pearson's chi-square yields 4.83, which with 4 df, has a p-value of 0.306, thus indicating an acceptable model fit. Misclassification error contributes from about 8% to 14% to the total variance in the estimates of the proportion of hatchery stock.

Design considerations

Design of an otolith reading program is complicated by misclassification error. An important consideration is the precision of the estimates, in particular the precision of the estimate of p. Table 5 shows the asymptotic standard error of $\hat{p}$ for various combinations of p, $\pi_{H|H}$, and $\pi_{W|W}$ for the three-reader model with unknown accuracies, and the one-, two-, and three-reader models with accuracies assumed known. Although this table is derived for a sample of 1000 otoliths, the ratio of any two standard errors within the table would be the same for any sample size (assuming the sample size is large enough to approximate the asymptotic conditions). It is evident that misclassification inflates the standard error over the usual binomial case (right-most column). The table also makes clear the increase in the uncertainty of estimating p when the accuracies also have

Table 3

Cross-classification data and results for 570 chum otoliths examined by three readers showing the parameter estimates and standard errors from the latent class model, followed by a comparison of the differences among reader pairs by using kappa and the latent class model (LCM) accuracy rates. The data show that the high agreement among readers as to hatchery and wild classification (e.g. HHH=406 and WWW=135) is reflected in the overall high accuracy rates estimated from the LCM. However the model also shows that reader 3 has a significantly lower accuracy rate in detecting hatchery marks ($\pi^{(3)}_{H|H}$=0.969) than the other readers.

Reading	Count	LCM Parameter	Estimate	SE
HHH	406	$\pi^{(1)}_{H\|H}$	0.998	0.002
HHW	13	$\pi^{(2)}_{H\|H}$	0.998	0.002
HWH	1	$\pi^{(3)}_{H\|H}$	0.969	0.008
WHH	1	$\pi^{(1)}_{W\|W}$	0.958	0.017
HWW	6	$\pi^{(2)}_{W\|W}$	0.986	0.010
WHW	2	$\pi^{(3)}_{W\|W}$	0.957	0.017
WWH	6	p	0.738	0.018
WWW	135			

Reader pairs	κ	SE	Difference in $\pi_{H\|H}$	SE	Difference in $\pi_{W\|W}$	SE
1 and 2	0.954	0.014	0.000	0.004	–0.028	0.020
1 and 3	0.882	0.022	0.029	0.009	0.000	0.024
2 and 3	0.901	0.021	0.029	0.009	0.028	0.020

Table 4

Cross-classification data for 2340 sockeye otoliths examined by two readers and stratified by four fishing districts, showing the estimates of the latent class parameters and their standard errors. Between-reader comparison is based on whether the difference in accuracy estimates are significantly different than zero. The results indicate that the readers were not statistically different in detecting hatchery marks ($\pi_{H|H}$) but were statistically different in detecting wild marks ($\pi_{W|W}$). LCM = latent class model.

	Fishing districts			
	108–30	108–50	106–41	106–30
HH	152	127	85	20
HW	11	9	21	5
WH	2	6	5	1
WW	271	382	832	411
n	436	524	943	437

LCM parameter	Estimate	SE	Reader difference	SE
$\pi_{H\ H}{}^{(1)}$	0.980	0.013	0.017	0.025
$\pi_{H\ H}{}^{(2)}$	0.964	0.021		
$\pi_{W\|W}{}^{(1)}$	0.984	0.005	–0.013	0.006
$\pi_{W\ W}{}^{(2)}$	0.997	0.003		
$p_{108–30}$	0.366	0.024		
$p_{108–50}$	0.257	0.020		
$p_{106–41}$	0.096	0.010		
$p_{106–30}$	0.047	0.011		

to be estimated in the three-reader case. For example, if $\pi_{H|H} = \pi_{W|W} = 0.8$ for all three readers, one would have to have almost twice (0.035/.019=1.84) the sample size to estimate a p of about 0.5. Once accuracy estimates for the readers are obtained, dropping one or even two readers may be appropriate, although the assumption must be made that the accuracy rates will be constant for the remainder of the program. Maintaining two readers will allow for that

Table 5

Asymptotic standard errors for the estimated proportion of marked fish, $\hat{p}$, for various combinations of accuracy rates in identifying hatchery fish, $\pi_{H|H}$, and wild fish, $\pi_{W|W}$, and mark proportion p, for a sample of 1000 otoliths. Values are reported for the cases where accuracy rates, π, are the same and assumed known for one, two, or three readers, and for the case where π's are estimated for three readers. Table illustrates how misclassification will increase standard errors in the estimate of hatchery proportion.

	$\pi_{H\|H}$	0.8			0.9			1.0	
	$\pi_{W\|W}$	0.8	0.9	1.0	0.8	0.9	1.0	0.8	0.9	1.0
	p									
3 readers	0.1	0.032	0.016	0.011	0.023	0.013	0.010	0.018	0.011	0.009
(π's estimated)	0.3	0.034	0.021	0.017	0.024	0.017	0.015	0.020	0.015	0.014
	0.5	0.035	0.023	0.019	0.023	0.018	0.016	0.019	0.016	0.016
	0.7	0.034	0.024	0.020	0.021	0.017	0.015	0.017	0.015	0.014
	0.9	0.032	0.023	0.018	0.016	0.013	0.011	0.011	0.010	0.009
3 readers	0.1	0.013	0.011	0.010	0.011	0.010	0.009	0.010	0.010	0.009
(π's known)	0.3	0.018	0.016	0.015	0.017	0.015	0.015	0.015	0.015	0.014
	0.5	0.019	0.018	0.016	0.018	0.017	0.016	0.016	0.016	0.016
	0.7	0.018	0.017	0.015	0.016	0.015	0.015	0.015	0.015	0.014
	0.9	0.013	0.011	0.010	0.011	0.010	0.010	0.010	0.009	0.009
2 readers	0.1	0.015	0.013	0.010	0.013	0.011	0.010	0.011	0.010	0.009
(π's known)	0.3	0.020	0.018	0.015	0.018	0.016	0.015	0.015	0.015	0.014
	0.5	0.022	0.019	0.016	0.019	0.018	0.016	0.016	0.016	0.016
	0.7	0.020	0.018	0.015	0.018	0.016	0.015	0.015	0.015	0.014
	0.9	0.015	0.013	0.011	0.013	0.011	0.010	0.010	0.010	0.009
1 reader	0.1	0.023	0.017	0.011	0.020	0.015	0.010	0.018	0.014	0.009
(π's known)	0.3	0.026	0.021	0.017	0.022	0.019	0.016	0.020	0.017	0.014
	0.5	0.026	0.022	0.019	0.022	0.020	0.017	0.019	0.017	0.016
	0.7	0.026	0.022	0.020	0.021	0.019	0.017	0.017	0.016	0.014
	0.9	0.023	0.020	0.018	0.017	0.015	0.014	0.011	0.010	0.009

assumption to be checked because there will now be extra degrees of freedom to assess goodness-of-fit (there are 3 df, but only one parameter, p, needs to be estimated). Estimates of p can still be obtained with one reader, but there can be no check of the assumptions. Also, there can be a significant increase in uncertainty in the estimate in using only one reader.

Discussion

There are numerous classification problems in fisheries that require the judgment of trained individuals. In many of those situations no "gold standard" is available to test those judgments, and it becomes necessary to apply other methods to determine the veracity of the classifications. Reading thermally marked otoliths is a particularly good example of this problem because thousands of classification decisions are needed each year to provide estimates of hatchery contributions.

The common approach for assessing the quality of the readings, in the absence of having samples of known origin, has been to collect independent and multiple readings on the samples, and to presume that agreement between readings can serve as a proxy for reading accuracy. Agreement indices such as κ are very easy to compute, and they have utility in that they can serve as flags to indicate reading problems. However, as was shown here, they also suffer difficulties in interpretation. Also, the indices in themselves do not provide inferences about the relative skill of different readers in pulling out a particular set of patterns.

Latent class models provide an approach with readily interpretable quantities for a modest computational cost. Classification accuracies or errors are direct, meaningful parameters unlike an index of agreement. In addition, estimates of p are available. These models can be readily extended to the case of more than two outcomes, e.g. multiple hatchery marks. These models could also be useful in other applications, such as in aging fish or in the identification of any character for which there is no "gold standard" (e.g. field identification of species or sex). A somewhat similar analysis has been proposed for aging (Richards et al., 1992), although the link to LCMs was not discussed. LCMs can handle fairly complicated situations, including ordered classes (Croon, 1990), continuous manifest variables, and parameter constraints (see Clogg, 1995, and Krzanowski and Marriott, 1995, for reviews).

We have not discussed the Bayesian approach to these problems in great detail, but we believe it has much to offer in that it can incorporate prior information, either

in the form of expert opinion (e.g. Demissie et al., 1998) or in the form of results of earlier analyses (e.g. Viana et al., 1993). Rather than assuming that estimated accuracies are "known," one can incorporate the uncertainty in the estimates into the prior distributions. In addition, the Bayesian approach does not rely on asymptotic results that may behave poorly with small samples. We have also not assessed the possible bias due to the lack of independence in the readings. When suitable software becomes available, this assumption should be checked.

In our examples above, misclassification error contributed relatively little to the overall uncertainty. In these applications, where estimates of hatchery contribution were used to make management decisions, the accuracy of readings were within an acceptable range. However, the criteria used to establish quality control standards in any program need to be developed in the context of how the information is to be used along with other sources of uncertainty.

In conclusion, we believe that the use of agreement measures in combination with latent class models can contribute significant information about both the proportions of interest and the quality control aspects of an otolith-marking program. Furthermore these approaches could have application to similar areas in fisheries which require judgments that are not free of error.

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Appendix

The following SAS (version 6.12) code was used to estimate parameters in the three-reader model discussed above. This program makes use of iteratively reweighted least squares to maximize the likelihood function. Observed values (e.g. the number of HHH) are equated with the corresponding expected value from the model and a weighted least squares fit is computed by using PROC NLIN. This computation is iterated to convergence of the parameter estimates. Weights are inverses of the predicted values at each iteration. Indicator variables for each possible outcome are generated so that a model in typical regression form can be written. Bounds on the parameter estimates may be needed to constrain the estimates to the appropriate intervals. Note that the asymptotic standard errors provided by SAS will be correct if the option SIGSQ=1 is specified. However, the printed degrees of freedom and the associated confidence intervals are not correct for this application. The residual weighted sum of squares listed by SAS is the chi-squared goodness-of-fit-statistic. The option, OUTEST, outputs point estimates and the the estimated covariance matrix for the parameters. SAS code for the multistrata model used in the second example is also available from the authors.

```
/* SAS Code for estimating 3-reader, 1-stratum model */

data a;
  array x{8} x1-x8;
  input y;
  ntot+y;                                   /* accumulating sample size */
  if _n_=8 then call symput('ntot',ntot);   /* put total into macro var */
  do i=1 to 8;
    if i=_n_ then x{i}=1; else x{i}=0;      /* set up indicator variables */
  end;
  cards;
 406        /* H H H */
  13        /* H H W */
   1        /* H W H */
   1        /* W H H */
   6        /* H W W */
   2        /* W H W */
   6        /* W W H */
 135        /* W W W */
;

proc nlin data=a nohalve sigsq=1 outest=est;        /* sigsq=1 for correct se's */
  parms a1=.9 a2=.9 a3=.9 b1=.9 b2=.9 b3=.9 p=.6;   /* starting values */
  e1=a1*a2*a3*p+(1-b1)*(1-b2)*(1-b3)*(1-p).         /* a is accuracy for H */
  e2=a1*a2*(1-a3)*p+(1-b1)*(1-b2)*b3*(1-p).         /* b is accuracy for W */
  e3=a1*(1-a2)*a3*p+(1-b1)*b2*(1-b3)*(1-p).
  e4=(1-a1)*a2*a3*p+b1*(1-b2)*(1-b3)*(1-p).
  e5=a1*(1-a2)*(1-a3)*p+(1-b1)*b2*b3*(1-p).
  e6=(1-a1)*a2*(1-a3)*p+b1*(1-b2)*b3*(1-p).
  e7=(1-a1)*(1-a2)*a3*p+b1*b2*(1-b3)*(1-p).
  e8=(1-a1)*(1-a2)*(1-a3)*p+b1*b2*b3*(1-p).
  model y=(e1*x1+e2*x2+e3*x3+e4*x4+e5*x5+e6*x6+e7*x7+e8*x8)*&ntot;
  bounds  0.5<=a1<=1, 0.5<=a2<=1, 0.5<=a3<=1, 0.5<=b1<=1, 0.5<=b2<=1,
          0.5<=b3<=1, 0<=p<=1;
   weight_=1/model.y;
run;
```

Abstract—Distribution, abundance, and several population features were studied in Ensenada de La Vela (Venezuela) between 1993 and 1998 as a first step in the assessment of local fisheries of swimming crabs. *Arenaeus cribrarius* was the most abundant species at the marine foreshore. *Callinectes danae* prevailed at the estuarine location. *Callinectes bocourti* was the most abundant species at the offshore. Abundances of *A. cribrarius* and *C. danae* fluctuated widely and randomly. Ovigerous females were almost absent. Adults of several species were smaller than previously reported. This study suggests that fisheries based on these swimming crabs probably will be restricted to an artisanal level because abundances appear too low to support industrial exploitation.

Local distribution and abundance of swimming crabs (*Callinectes* spp. and *Arenaeus cribrarius*) on a tropical arid beach

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Swimming crabs of the family Portunidae are common in coastal habitats in tropical, subtropical, and temperate regions. Species of the genus *Callinectes* are widely distributed in the neotropics and subtropics (Norse, 1977; Williams, 1984) where they are a key resource in local fisheries (Ferrer-Montaño, 1997; Fischer, 1978; Oesterling and Petrocci, 1995) and are important in trophic relations of fish and organisms of sandy and sandy-mud bottoms (Arnold, 1984; Lin, 1991), and in seagrass meadows (Orth and van Montfrans, 1987; Wilson et al., 1987). Several species of portunids have been thoroughly studied (e.g. *C. sapidus*), and many aspects of their biology, ecology, biogeography, and fisheries (including types of fisheries and the commercial exploitation of these species as "soft-shell" crabs) have been addressed, (Taissoun, 1969, 1973a, 1973b; Norse, 1977, 1978; Norse and Estevez, 1977; Perry and Van Engel, 1979; Williams, 1984; Smith et al., 1990). However, some species remain poorly known. Knowledge about species of *Callinectes* is mainly restricted to temperate regions, in spite of their commercial importance in the Caribbean. Furthermore, although several features of the speckled swimming crab, *Arenaeus cribrarius*, have been studied in Brazil, such as relative growth and some ecological aspects of populations (Avila and Branco, 1996; Pinheiro et al., 1996, 1997; Pinheiro and Fransozo, 1993, 1998, 1999), and elsewhere, such as its role in the trophic web in a sandy beach in South Carolina and its larval development (Stuck and Truesdale, 1988; DeLancey, 1989), as far as we know there are no published accounts of its abundance in the southern Caribbean.

Several studies of portunids have been conducted on Venezuelan coasts (Taissoun, 1969, 1973a, 1973b; Rodríguez, 1980; Scelzo and Varela, 1988; Carmona-Suárez and Conde, 1996), including species that are commercially important at an industrial level and as a mainstay for artisanal and subsistence fisheries in many coastal villages (Ferrer-Montaño, 1997; Conde and Rodríguez, 1999). A few studies with emphasis on biogeographical, taxonomic, and morphometric features of the family have been conducted in Lake Maracaibo, a polyhaline system (Taissoun 1969, 1972, 1973a, 1973b; Schubart et al., 2001). Seven species of *Callinectes* and the speckled swimming crab, *A. cribrarius*, have been listed for the State of Falcón (Carmona-Suárez and Conde, 1996), which is characterized by protracted desolate coasts, sandy and sand-mud beaches (Carmona and Conde, 1989), and an abnormally arid climate (Lahey, 1973). Lake Maracaibo, which is roughly 240 km west of Ensenada de La Vela, has the largest crab and crabmeat industry in Venezuela. Most of it is exported to the United States, where it accumulated a total value of US$ 6.2 million in 1992 (Oesterling and Petrocci, 1995). The main crab species captured in this area is *C. sapidus*. Crabs have also been harvested near Punto Fijo and Coro, the latter just 10 km from Ensenada de La Vela. In this locality, *C. bocourti* is harvested by artisanal fishermen (senior author, personal obs.). In spite of this, nothing is known about the abundance, microdistribution, and population traits of

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swimming crabs on these arid beaches. Our study is thus important both ecologically and as a preliminary assessment of stock levels and their potential for sustainable exploitation. Also, few studies address the guild structure of portunid crabs in the Caribbean Basin (Taissoun, 1969, 1973a; Moncada and Gómez 1980; Buchanan and Stoner 1988), in spite of their importance to fisheries.

The purpose of our study was to widen our knowledge of the population biology of *A. cribrarius* and various species of *Callinectes* in the Southern Caribbean. We quantified the distribution and population aspects of several species of *Callinectes* and *A. cribarius* on a sandy beach and in a small estuary located on an arid shoreline in Falcón, western Venezuela. We present data on the distribution and abundance of a guild of portunids, their physical correlates, and some population characteristics of the dominant species in marine and estuarine habitats.

Materials and methods

Sampling area

Ensenada de La Vela (11°27′N, 69°34′W) is a small cove located on the central coast of the State of Falcón in western Venezuela next to Istmo de Médanos, a narrow low-lying isthmus that links Península de Paraguaná to the mainland (Fig. 1). Ensenada de La Vela lies at the center of a region that extends from eastern Panamá to the Paria Peninsula in eastern Venezuela that has been regarded as abnormally dry (Lahey, 1973). In Falcon's western coastal strip and in the Península de Paraguaná, rainfall is scarce and seasonal with peaks during October–December, when nearly 50–60% of the precipitation occurs. The average yearly rainfall on the peninsula is 400 to 600 mm (Goddard and Picard, 1976), although in some localities the environment is harsher with a mean of 256.8 mm (Conde and Díaz, 1992b). The mean air temperature is 27.7°C, and the average wind speed is 10 kph and seasonal (Goddard and Picard, 1976). No mangroves, coral reefs, or seagrass beds appear at Ensenada de La Vela.

Sampling procedures

All samplings were carried out outside the fishing areas used by local fishermen. Our study was conducted in three stages. During the first and second stages, crabs were sampled at two major biotopes, where three open-water marine stations at the foreshore and one enclosed estuarine station were set. Station 1 was located on the eastern corner of Ensenada de La Vela, the most protected area, where the surf action is extremely weak. Station 2 was also located in the marine front, but next to the inlet of a natural estuarine impoundment where a nearby basin drains. Station 3 was established in this estuarine area, which is not freely connected to the ocean because its exchange mouth is blocked by a sandbar for most of the year. Station 4 was also set at the oceanic front, but in a zone exposed to rugged surf, next to an area that has the strongest wave action in Venezuela. Marine stations were characterized by sandy bottoms, low-transparency waters, and low-lying coastal profiles, whereas the estuarine station was mainly composed of muddy substrate, and had little water movement. Most of the bottom was devoid of vegetation and was interspersed with scarce flat rocky patches. As a whole, some 300 m of shoreline were trawled during each sampling.

During the first stage of sampling, trawling and environmental measurements were conducted monthly at each station from January 1993 to December 1994. Field campaigns included both rainy and dry seasons. Crabs were collected using a 7-meter long and 1.5-m tall hand seine (locally known as a "chinchorro"), with a mesh diameter of 1.0 cm. The hand seine was trawled perpendicular to the coast by two persons walking alongside the net in a 20-m long strip, parallel to the coast, at a depth ranging from 1 to 1.5 m. We repeated this process four times consecutively at approximately the same site. This is the procedure that local fishermen use to capture shrimp and fish to optimize fishing effort. Because waves break and depth does not exceed 1.5 m at our sampling sites, these sites were unsuitable for the other types of fishing gear used in other studies for capture of swimming crabs, such as crab pots, trot lines, otter trawls, and dip nets, among others (Sholar, 1979; van Montfrans et al., 1986; Prager et al., 1990; Ryer et al., 1990; Hsueh et al., 1992). Our method was also used by Carmona-Suárez and Conde (1996) to inventory brachyuran crabs in the State of Falcón, Venezuela. After each trawl at a given station, captured crabs were put in a bucket until sampling at that specific site was completed. When all four trawls were completed and the data were recorded, crabs were returned alive to the same place.

Because the behavior of some swimming crabs has been hypothesized to follow daily cycles of burrowing in the substratum during the day and of emerging at night (Warner, 1977; Fischer, 1978), we conducted a second stage of samplings from September 1997 to February 1998 at the same sites. We sampled during the day and the night of the same day or on consecutive days to determine if there were any systematic differences in the composition of the guild, in the abundance, size, and sex ratios of crabs, and to detect potential biases introduced by the sample design used in stage 1. The gear and sampling design for stage 2 was the same used during stage 1, but we were unable to collect crabs at the estuarine station because of a discharge of untreated domestic sewage at the beginning of 1997.

The purpose of the third sampling stage was to assess if guild composition and other characteristics were influenced by depth or by distance from the coast. Three new stations (inshore, midshore, and offshore) were sampled simultaneously in August 1998 and from June to July 1999, from the foreshore oceanward at intervals of 50 m (Fig. 1). The depth at the inshore station was ~1.5 m, and the depths at the mid- and offshore stations were ~2.5–3 m. During this stage, two crab pots with fish bait (as described by Oesterling, 1984) were deployed at each station for approximately 12 hours during the day, and for the same amount of time during the night, except in August 1998, when pots were deployed for 6 hours during the day and

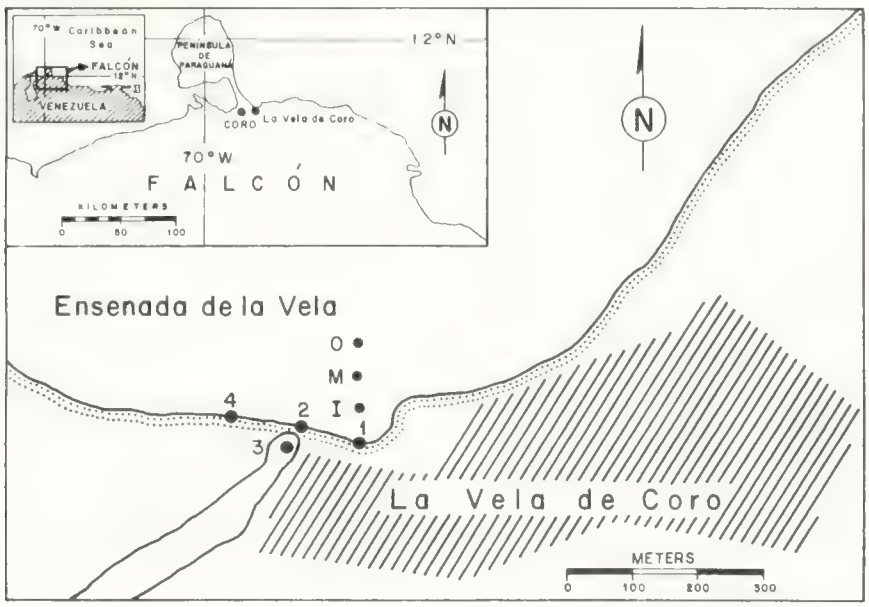

Figure 1

Map of sampling sites at Ensenada de La Vela, State of Falcón, Venezuela. Stations 1 to 4: = foreshore sampling sites (stages 1 + 2); I = inshore sampling site, M = midshore sampling site, O = offshore sampling site (stage 3).

other 6 hours during the night. This process was carried out for three to four consecutive days. No monthly or seasonal samples were taken at these three offshore stations.

Crab identification and characterization

Crabs from each stage were sorted to species, their sex was determined, and each crab was measured immediately after capture. Carapace length was measured with a 0.5-mm-precision Vernier caliper. This measurement was selected instead of carapace width because lateral spines can be abraded, making this measure of body size unreliable. This measurement method has also been used by Moncada and Gómez (1980) and Williams (1984). Animals were identified by using a key compiled from the information and keys in Taissoun (1969, 1973b), Fischer (1978), Rodríguez (1980), and Williams (1984). Juvenile females are identified by a triangular pleon and adults by a semicircular pleon. Adult males have an abdomen detached from the sternum; juveniles do not.

Environmental variables and data analysis

At each station, from January 1993 to December 1994, surface water temperature and salinity were measured with a 0.5°C precision mercury thermometer and a temperature-compensated hand refractometer, respectively. Dissolved oxygen was determined from November 1993 up to December 1994 with a YSI® dissolved oxygen meter. During the second and third sampling stages (1997–98 and 1999) only salinity values were recorded. Rainfall data were retrieved from the raw records of the meteorological station belonging to the Ministry of the Environment and Natural Resources (Venezuela), located at Coro Airport, about 10 km west of the sampling sites.

Population dynamics were analyzed only for the most abundant species that appeared regularly during each sample. Dissimilarities in body size between species were compared by using a two-tailed Student's *t*-test of the differences between two means. Sets of continuous variables were checked for normality with the Kolmogorov-Smirnov goodness-of-fit test. Homogeneity of variances of groups of data to be compared by *t*-tests was checked with Bartlett's test (StatSoft, 1992; Sokal and Rohlf, 1995). In those cases where normality or homoscedasticity were not met, data were log-transformed. Multiple comparisons were performed with the Tukey-Kramer method. The degree of association between crab abundance and environmental variables was assessed with the product-moment correlation coefficient. To compare abundance distributions between stations and diel samplings, R×C tables were analyzed with the *G*-test of independence. No extrinsic hypothesis were considered.

To describe portunid guild composition, several diversity indices were used: Simpson's, Shannon-Weaver, and Hill's numbers (N1 and N2) (Ludwig and Reynolds, 1988). Simpson's index gives the probability that two individuals drawn from a population belong to the same species. The Shannon-Weaver index measures the average degree of uncertainty in predicting to what species an individual chosen at random would belong. Hill's numbers N1 and N2, whose units are number of species, show how many common and very common species appear in a guild or community and lessen the weight of rare species.

Results

Rainfall patterns

In 1993 and 1994, mean annual rainfall at Coro was 228.4 and 58.7 mm, respectively. Precipitation, which was below the historical yearly average (403.5 mm; 1921–87), was distributed irregularly. Wet and dry seasons did not show any evident pattern (Fig. 2). In 1993, rains peaked in April and May, and secondary peaks occurred in July and November, whereas in 1994, precipitation reached a maximum during July–August and there was a lesser amount in January. During the latter year, four months were entirely deprived of rain (Fig. 2).

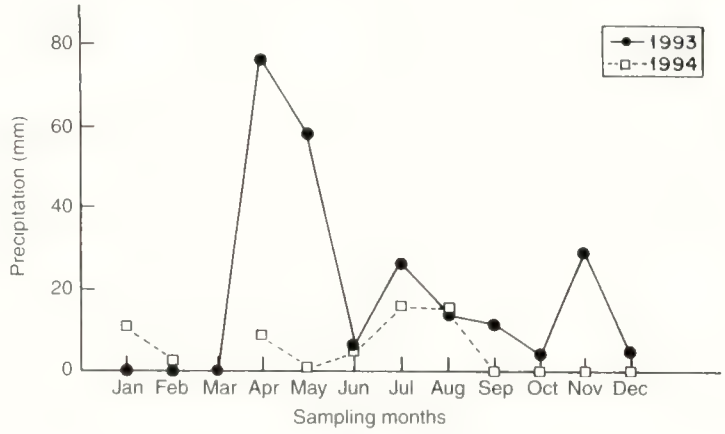

Figure 2
Rainfall in Coro (Falcón, Venezuela) during 1993 and 1994.

Physicochemical variables

Water temperature means and ranges from two-year monthly measurements at the estuarine and three foreshore stations are shown in Figure 3A. Temperature did not differ significantly among marine sites. However, mean water temperature was higher in the estuarine site (Table 1), with an average of 29°C, and so was the range, 25–34°C (Fig. 3A).

Mean salinity and its range varied slightly between marine stations (Fig. 3). The highest value was reached at station 1 and the lowest at stations 1 and 2. Salinity was significantly lower in the estuarine site (Table 1), but its range was much wider than at any other site (Fig. 3). Salinity varied very little over time at the marine stations, with the exceptions of the beginning of 1993, when salinity dropped to nearly 30‰, and November–December 1994 and the onset of 1994, when the water reached hypersaline levels (Fig. 3). Salinity at the estuarine site varied widely through time, peaking in February 1993, January 1994, and August 1994. Minima were registered in September 1993 and July 1994 (Fig. 3).

Mean dissolved oxygen was highest at station 2 and lowest at the estuarine site, where similarly the lowest absolute value observed throughout the study was recorded (Fig. 3). At the marine stations, dissolved oxygen had a smaller range than at the estuarine site, whereas the range was shifted to lower values. Oxygen increased steadily from the end of 1993 until the end of 1994, when concentrations plunged at stations 3 and 4, and less abruptly at station 1. At station 2, the oxygen concentration increased to a maximum value at the end of the year (Fig. 3). However, no significant differences in dissolved oxygen were found between stations (Table 1).

Table 1
One-way ANOVA and Tukey honest significant difference test between three foreshore (stations 1, 2, and 4) and the estuarine station (station 3) in Ensenada de La Vela (1993–94). M = mean.

Temperature: df = 84; F = 4.576; P=0.005*

Stations	1 M=27.418	2 M=27.60	3 M=28.968	4 M=27.532
1		0.982	0.010*	0.995
2	0.982		0.029*	0.999
3	0.010*	0.029*		0.020*
4	0.995	0.999	0.020*	

Salinity: df = 87; F = 47.153; P=0.001*

Stations	1 M=37.409	2 M=36.56	3 M=19.522	4 M=36.391
1		0.966	0.0001*	0.942
2	0.966		0.0001*	0.100
3	0.0001*	0.0001*		0.0001*
4	0.942	0.100	0.0001*	

Dissolved oxygen: df = 52; F = 1.296; P=0.286 not significant

Stations	1 M=7.814	2 M=8.143	3 M=7.021	4 M=7.736
1		0.943	0.535	0.999
2	0.943		0.236	0.899
3	0.535	0.236		0.619
4	0.999	0.899	0.619	

Distribution, abundance and diversity

Surf zone A total of 478 swimming crabs were collected during the first stage of our study in the surf and at the estuarine pond (Table 2). Overall, *A. cribrarius* and *C. danae* dominated. They were followed by *C. bocourti*, *C. sapidus*, *C. exasperatus*, *C. maracaiboensis*, and *C. larvatus*. At the marine biotope, where five species of portunids were caught throughout our study, *A. cribrarius* was the prevailing species, with shares of 77.5%, 73.7% and 86.5%, at stations 1, 2, and 4, respectively. The second most abundant species

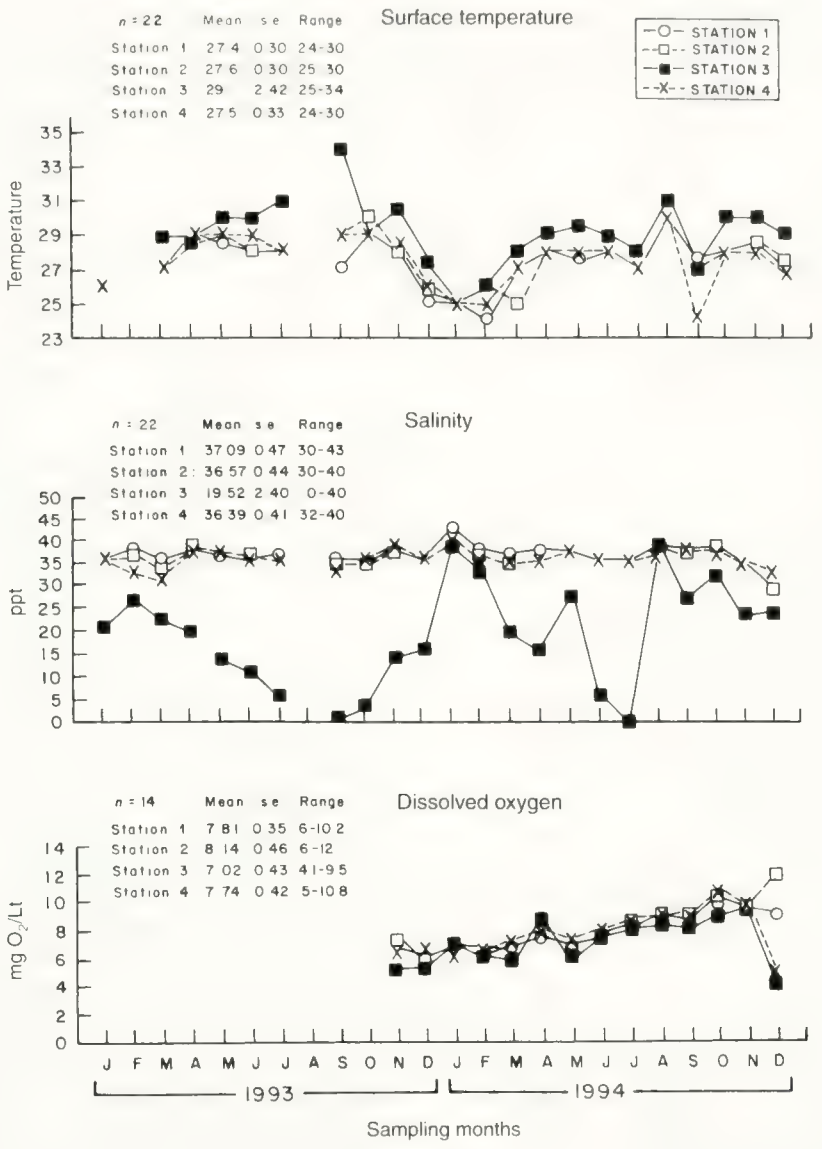

Figure 3

Surface temperature, salinity, and dissolved oxygen at the foreshore and estuarine stations in Ensenada de La Vela (Falcón, Venezuela).

at the marine stations was *C. danae* (Table 2). The highest number of species, six, was recorded at the estuarine site, where *C. danae* clearly dominated with a relative abundance of 75.2%, followed by *C. bocourti* (14.1%), *C. exasperatus* (4.5%), *C. sapidus* (2.5%), *C. maracaiboensis* (2.0%) and *C. larvatus* (1.5%). *Arenaeus cribrarius* was absent from the estuarine site. Overall, the highest diversity (Shannon-Weaver index) was registered at the estuarine station, followed by station 2, station 1, and finally station 4, the most exposed tract. Hill's diversity number 1 (N1), which indicates abundant species, was also highest at the estuarine station 3, followed by stations 2, 1, and 4 (Table 2). In a comparison of the two main biotopes (all three marine stations vs. the estuarine station) for the most frequent species (*A. cribrarius* and *C. danae*), their abundance was dependent on salinity (G=306; df=1, P<0.005). However, their abundance was independent of wave exposure, when only the stations in the marine biotope were considered (G=5.624; df=2, 0.05 >P>0.1).

Offshore A total of 173 swimming crabs were caught with crab pots. Abundance was highest at the seaward-most station, followed by the inshore and midshore stations (Table 3). The average number of individuals per pot at each site followed a similar sequence (offshore: 5.9 individuals/pot; inshore: 1.75 ind/pot; midshore: 1.5 ind/pot). Differences in abundance between offshore and inshore and between offshore and midshore stations were

Table 2

Overall abundance (no of crabs) and diversity indexes for swimming crabs at seaside in Ensenada de La Vela (Venezuela).

		Station 1	Station 2	Station 3	Station 4	Totals (%)
A. cribrarius		86	70	0	64	220 (46)
C. danae		19	22	149	7	197 (41.2)
C. bocourti		0	2	28	1	31 (6.5)
C. maracaiboensis		0	0	4	0	4 (0.8)
C. sapidus		6	1	5	1	13 (2.7)
C. exasperatus		0	0	9	1	10 (2.1)
C. larvatus		0	0	3	0	3 (0.6)
Number of specimens		111	95	198	74	478
Number of species		3	4	6	5	
Simpson (λ')		0.6292	0.5928	0.5876	0.7542	
Shannon-Weaver (H')		0.6580	0.6930	0.8660	0.5230	
Hill's numbers	N1	1.9300	2.0000	2.3780	1.6870	
	N2	1.5894	1.6868	1.7018	1.3260	

Table 3

Overall abundance (no. of crabs) and diversity indexes for swimming crabs captured with crab pots in Ensenada de La Vela (Venezuela).

		Inshore	Midshore	Offshore	Totals
C. bocourti		30	30	69	129
C. maracaiboensis		2	4	13	19
C. danae		3	1	8	12
C. ornatus		6	3	2	11
C. sp. (unidentified)		0	2	0	2
Number of specimens		41	40	92	
Number of species		4	5	4	
Simpson (λ')		0.5537	0.5705	0.5860	
Shannon-Weaver (H')		0.8485	0.8823	0.7879	
Hill's numbers	N1	2.3361	2.4164	2.1987	
	N2	1.8062	1.7528	1.7065	

significant, whereas the difference between inshore and midshore was not. Overall, four species were caught, but *C. bocourti* prevailed at all the stations with at least 73.2% of the total quantity (Table 3). Frequency of crabs by species varied significantly with the distance of the station to the shore (G=17.024, 0.05 >P>0.01, df=8). *C. bocourti* maintained a constant presence through the three stations, ranging from 73.2 to 75.0% of total crabs at each station, the abundance of *C. maracaiboensis* increased seaward, and the abundance of *C. ornatus* decreased. *Callinectes danae* did not show any trend.

In this set of samples, taken at a distance from the shoreline, the highest diversity (Shannon-Weaver index) was registered at the midshore station, closely followed by the inshore station and the offshore station. Hill's diversity number 1 (N1), which indicates abundant species, was also highest at the midshore station, followed by inshore and offshore stations (Table 3).

Temporal variability

Because data for *C. bocourti*, *C. sapidus*, *C. exasperatus*, *C. maracaiboensis* and *C. larvatus* were too scarce to allow useful analysis, temporal variability of the abundance at the surf and at the estuarine pond was examined only for *A. cribrarius*, *C. danae*, and for total crabs. Temporal variability of the abundances of these species are shown in Figure 4. Abundances fluctuated widely and randomly throughout our study. The density of *A. cribrarius* peaked in April, July, and October 1993, as well as in February and October 1994 (Fig. 4). In the estuarine site, *C. danae* abundance peaked in May and October 1993, as well as in February, April, August, and November 1994 (Fig. 4). In the marine sites, *C. danae* abundance was considerably lower and maxima occurred in June, September, and October 1993, and in May and October 1994 (Fig. 4). No significant correlations were found between abundances of these two species and rainfall, water temperature, salinity, and dissolved oxygen (Table 4). However, when total crabs were regressed against rainfall at the estuarine site and oxygen at the foreshore, correlations were significant (Table 4). The negative correlation of this latter factor reached almost significant levels for both species at the marine ecotope.

Diel variations

Surf zone A total of 196 crabs were caught with hand seines at the foreshore during September 1997–February 1998 samplings: 82 crabs at night and 114 during the day (Table 5). Six species appeared in the diurnal samples (*A. cribrarius, C. danae, C. bocourti, C. larvatus, C. maracaiboensis* and *C. sapidus*), one of which (*C. sapidus*) did

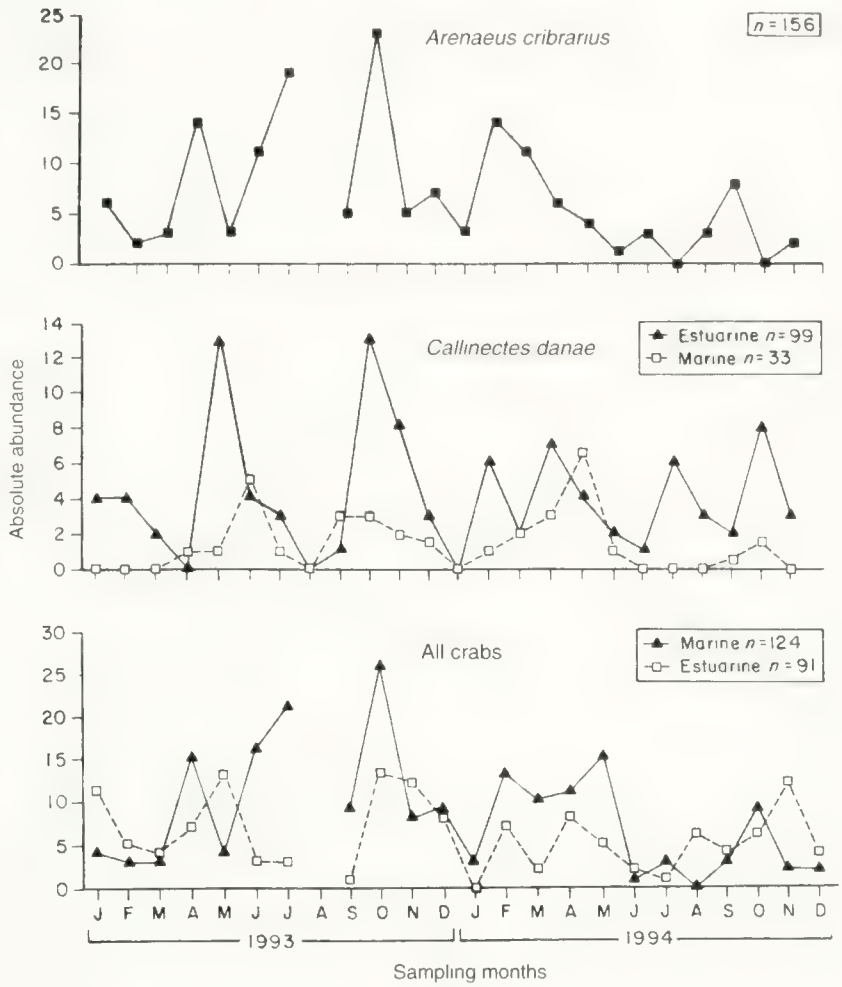

Figure 4

Abundance of *Arenaeus cribrarius*, *Callinectes danae*, and total captured crabs in Ensenada de La Vela (Falcón, Venezuela).

not appear at night. *Arenaeus cribrarius* was the dominant species followed by *C. danae*, during both diurnal and nocturnal samplings, whereas *C. maracaiboensis, C. bocourti, C. larvatus*, and *C. sapidus* were present in very low numbers. Guild composition did not differ significantly between day and night (G=1.630; 0.90>P>0.50; df=5), nor did the average number of individuals per trawl (0.86 vs. 0.62; t=1.702; 0.10>P>0.05; df=262). In both dominant species, *A. cribrarius* and *C. danae*, the average size of crabs caught during daylight hours (Table 5) did not differ significantly from those collected at night, nor did the size frequency distributions (G=3.820; df=4; 0.50>P>0.10). Sex ratios of these two species did not show significant diel differences either (G=0.030; 0.90>P>0.50; df=1; G=2.750; 0.50>P>0.10; df=1, respectively).

Offshore A total of 64 crab pots were deployed, 32 during each period. Four species were caught during both day and night (*C. bocourti, C. maracaiboensis, C. ornatus*, and *C. danae*). A total of 89 crabs were caught during the day and 84 at night (Table 6). *Callinectes bocourti* comprised 73.8% and 75.3% of the abundance during the day and night, respectively, followed by *C. maracaiboensis* (15.5% and 6.7%). No differences in guild composition or sex ratios were found between day and night samples at each of the sites (Table 6). Crab species did not show differences in carapace length between day and night captures (*C. bocourti*, t=0.704, P>0.05, df=155; *C. maracaiboensis*, t=1.355, P>0.05, df=13; *C. ornatus*, t=0.881, P>0.05, df=9; *C. danae*, t=1.811, P>0.05, df=10). Kolmogorov-Smirnov tests run for normality of carapace length distribution for species at the offshore station compared between day and night samples, were statistically nonsignificant.

Sex ratios and ovigerous females

At the foreshore, all the species had male-biased overall sex ratios (Table 7), although only *A. cribrarius*, *C. danae*

Table 4

Correlations between crab abundances and rainfall, salinity, temperature, and dissolved oxygen variables. ns = not significant.

Species	Biotope	Rainfall			Salinity			Temperature			Oxygen		
		r	*n*	Significance	r	*n*	Significance	*r*	*n*	Significance	*r*	*n*	Significance
Total crabs	Marine	0.1389	25	ns	–0.0634	34	ns	0.0634	33	ns	–0.4538	25	0.05>*P*>0.01
	Estuarine	0.4028	25	0.05>*P*>0.01	0.0408	34	ns	0.0774	33	ns	0.0620	25	ns
Callinectes danae	Marine	–0.0904	25	ns	0.0107	34	ns	0.1786	33	ns	–0.3155	25	ns
	Estuarine	0.1336	25	ns	0.0231	34	ns	0.2278	33	ns	0.1653	25	ns
Arenaeus cribrarius	Marine	–0.0904	25	ns	–0.0624	34	ns	0.0321	33	ns	0.3389	25	ns
	Estuarine	----------			----------		Absent	----------			----------		

and *C. sapidus* deviated significantly from the normal Mendelian ratio. Sex ratios for *C. bocourti* and *C. exasperatus* did not differ significantly from equality, possibly because of low sampling numbers for these species. In the estuarine site, none of the sex ratios deviated significantly from an even proportion, although *C. danae* did show a slight bias toward males (Table 7).

No berried females appeared at the foreshore nor at offshore stations. Only two ovigerous females were caught during our study; both were *C. danae* and were collected at the estuarine site in March 1994 (CL [carapace length]: 32.4 mm), and in May 1994 (CL: 43.25 mm).

Body size

Table 8 shows the carapace length (mm) of the most abundant crab species at the foreshore and estuarine stations in Ensenada de La Vela. *Callinectes danae* from the foreshore stations were larger than those from the estuarine site (t=3.799, P<0.05, df=185). The mean cephalothorax length in this species from the foreshore stations was 29.75 mm, whereas in the estuarine zone, crabs averaged 25.16 mm. The average size of adult females from the estuarine station did not differ significantly from those at the foreshore stations. Adult males from the foreshore stations, however, were significantly larger than those from the estuarine site. Male and females sizes did not differ significantly in the foreshore stations, whereas at the estuarine site females were significantly larger (Table 8). Average carapace length of *A. cribrarius* (n=216) was 20.10 (range: 9.48–56.55; SE: 0.496). Juvenile females were significantly larger than juvenile males (t=5.02; P<0.001; df=148). Body size characteristics of *C. bocourti* are shown in Table 8. No differences in size between adult *C. bocourti* males and females from the estuarine site were found (t=0.187; P>0.5; df=14). All Kolmogorov-Smirnov tests run for normality of carapace length distribution for species that were compared at the foreshore and estuarine stations, were statistically nonsignificant.

Discussion

Of the nine species of *Callinectes* that have been reported for the tropical Western Atlantic (Williams, 1984), seven appeared at the foreshore of Ensenada de La Vela during our study. The species with the widest distributions were *C. danae* and *C. sapidus*, which were the only ones to appear at all the stations by the sea margin. *Callinectes maracaiboensis* and *C. larvatus* had the most restricted distribution, occurring only in the estuarine site, and *C. exasperatus* was present only in the estuary and at one of the marine stations. At the marine foreshore stations, *A. cribrarius* was the dominant species, with a share of 78% of the total catch in this ecotope, whereas *C. danae* (19%) was the second most abundant species. Meanwhile, in the estuarine site, where *A. cribrarius* was absent, *C. danae* was the prevailing species, followed by *C. bocourti*. Overall, the highest diversity was registered at the estuarine station, whereas at the foreshore the highest diversity was recorded in the

Table 5

Body size (carapace length in mm) and species abundance during diel observations at the foreshore of Ensenada de La Vela (1997–98). Percentages are given in parentheses in "Abundance" column.

Species	Period	Abundance	Mean body size	SE
A. cribrarius	day	91 (79.8)	19.14	0.94
	night	59 (72.0)	19.38	1.24
C. danae	day	17 (14.9)	21.92	1.89
	night	16 (19.5)	23.09	2.45
C. bocourti	day	1 (0.9)	21.3	—
	night	2 (2.4)	33.83	11.4
C. maracaiboensis	day	2 (1.8)	47.45	9.10
	night	4 (4.9)	37.28	6.05
C. larvatus	day	2 (1.8)	30.55	2.25
	night	1 (1.2)	15.65	-
C. sapidus	day	1 (0.9)	38.4	-
	night	0	—	—
Total	day	114		
	night	82		

Table 6

Distribution of species abundance (no. of crabs found) at the offshore stations during diel samplings and comparisons of sex ratios (all sites pooled).

		C. bocourti	*C. maracaiboensis*	*C. danae*	*C. ornatus*	*C.* sp.[1]	Totals	*G* (df=4)	Significance
Inshore	night	12	2	1	1	0	16	5.238	0.50>*P*>0.10
	day	18	0	2	5	0	25		
Midshore	night	18	3	0	2	2	25	4.226	0.50>*P*>0.10
	day	12	1	1	1	0	15		
Offshore	night	32	8	1	2	0	43	8.506	0.10>*P*>0.05
	day	37	5	7	0	0	49		
Total	night	62	13	2	5	2	84	7.940	0.10>*P*>0.05
	day	67	6	10	6	0	89		
Overall totals		129	19	12	11	2	173		

Sex ratios	*G*	Significance
C. bocourti	0.01	0.975>*P*>0.9
C. maracaiboensis	0.642	0.5>*P*>0.1
C. danae	0.07	0.9>*P*>0.5
C. ornatus	2.864	0.1>*P*>0.05

[1] Unidentified species.

most protected marine stations (2 and 1) followed by station 4, which is located at the most exposed tract. The values of Hill's diversity number 1 (N1) demonstrated a similar pattern and indicated that the number of abundant species was close to two at stations 2 and 3, slightly above this value at the estuarine station, and below at the most exposed station. Offshore guild composition was substantially different from that at the sea margin, as shown by pot samplings. Although several species were common to the three biotopes, each habitat had a distinctive dominant species: *Arenaeus cribrarius* at the surf zone (stations 1, 2, and 4), *C. danae* (station 3) in the estuarine pond, and *C. bocourti* offshore. Because different sampling gears were used at the sea border and offshore because of practical

reasons, comparisons should be regarded as qualitative. However, artisanal fishermen do harvest *C. bocourti* when using beach seines in the areas next to our crab pot stations (senior author, personal obs.).

Inshore-offshore zonations of species at Ensenada de La Vela diverged from the gradients compiled by Norse and Fox-Norse (1979) for other areas in the Caribbean. In many localities, *C. bocourti, C. sapidus,* and *C. maracaiboensis* (the so-called *bocourti* group) are known to inhabit the waters by the seaside, whereas *C. marginatus* and *C. ornatus* are found at the seawardmost zone, and *C. danae* occupies the intermediate area. However, our patterns of

Table 7

Sex ratios for portunids captured in Ensenada de La Vela (1993–94).

	Male:female	Ratio	*G*	df	Significance
Marine stations					
A. cribrarius	155:61	2.5:1	21.607	1	$P<0.005$
C. danae	34:11	3.1:1	6.272	1	$0.01>P>0.025$
C. bocourti	0:1	0:1	—	—	—
C. sapidus	7:0	7:0	5.232	1	$0.01>P>0.025$
C. exasperatus	1:0	1:0	—	—	—
Estuarine station					
C. danae	79:63	1.3:1	0.900	1	$0.5>P>0.1$
C. bocourti	13:15	0.9:1	0.070	1	$0.9>P>0.5$
C. sapidus	2:3	0.7:1	0.088	1	$0.9>P>0.5$
C. exasperatus	7:2	3.5:1	1.405	1	$0.5>P>0.1$
C. larvatus	2:1	2:1	—	—	—
C. maracaiboensis	2:2	1:1	—	—	—

Table 8

Carapace length (mm) for the most abundant species at the foreshore and estuarine stations in Ensenada de La Vela (Venezuela), and comparison of carapace sizes. ns = not significant.

	Marine stations					Estuarine station			
Callinectes danae	*n*	Mean	Range	SE	*Callinectes danae*	*n*	Mean	Range	SE
Juvenile females	8	24.6	14.92–32.7	2.099	Juvenile females	37	22.6	11.28–35.6	1.069
Adult females	3	39.6	36.58–42.0	1.619	Adult females	26	39.8	31.45–47.4	0.832
Juvenile males	14	19.5	8.5–32.4	2	Juvenile males	43	15.8	7.62–27.4	0.691
Adult males	20	39.1	7.42–56.7	2.869	Adult males	36	23.7	10.4–48.4	1.897
	Marine stations only					Estuarine station only			
Arenaeus cribrarius	*n*	Mean	Range	SE	*Callinectes bocourti*	*n*	Mean	Range	SE
Juvenile females	61	22	11.3–36.94	0.831	Juvenile females	7	23.1	11.8–34.4	3.251
Adult females	No adult females				Adult females	10	41	34–45.1	1.126
Juvenile males	89	17.6	10.25–28.64	0.459	Juvenile males	4	19.6	16.6–23	1.314
Adult males	66	21.8	9.48–56.55	1.213	Adult males	6	41.8	24.4–56.5	5.035

		t	df	Significance
C. danae (all crabs)	foreshore/estuarine	3.799	185	$P<0.05$
C. danae (adult females)	foreshore/estuarine	0.065	27	ns
C. danae (adult males)	foreshore/estuarine	4.653	54	$P<0.001$
C. danae (foreshore stations)	females/males	0.766	43	ns
C. danae (estuarine station)	females/males	6.297	140	$P<0.001$

abundance for *Callinectes* species are similar to another Caribbean locality (Buchanan and Stoner, 1988): Laguna Joyuda (Puerto Rico). All the *Callinectes* spp. recorded in this coastal estuarine lagoon were also present in the estuarine station of Ensenada de La Vela. *Callinectes danae* was the dominant species in both sites, whereas *C. exasperatus* and *C. larvatus* were present in low numbers. *Callinectes maracaiboensis* was very scarce at Ensenada de La Vela, but it was not reported at all in Laguna Joyuda (Buchanan and Stoner, 1988), although Buchanan and Stoner cautioned that specimens of this species might have been misclassified and listed as *C. bocourti*. On the other hand, the high abundance of *A. cribrarius* at the marine front of Ensenada de La Vela differed from that of other studies in the Caribbean and Gulf of Mexico, where this species has been reported in low numbers. For instance, in the SW Gulf of Mexico *A. cribrarius* was less than 1% of the total portunid community (García-Montes et al., 1988). In Laguna de Términos (Mexico), a polyhaline coastal lagoon, four species of *Callinectes* were found in a population survey conducted during a whole year, but no individuals of *Arenaeus* were reported (Román-Contreras, 1986). In the same lagoon, Sánchez and Raz-Guzmán (1997) caught a single individual of *A. cribrarius* out of 986 specimens collected over a 17-year span. The differences probably are probably due to the polyhaline conditions at these settings, thus restricting the viability of *A. cribrarius*. However, in temperate sandy beaches, this species can be very common. On Bogue Banks, in North Carolina, *Arenaeus cribrarius* ranked as the most important brachyuran in a high-wave-energy sandy beach (Leber, 1982). In the surf zone at Folly Beach, South Carolina, *A. cribrarius* was one of the dominant brachyuran crabs during the summer and also a key predator of benthic organisms (DeLancey, 1989). *A. cribrarius* is considered to be well-adapted to marine and slightly hypersaline salinity regimes and to habitats with heavy surf and sand scouring in shallow coastal waters (Fischer, 1978; Williams, 1984). This fact was evident in our study, in which *A. cribrarius* was abundant and clearly constrained to a narrow strip in the surf zone.

Our results suggest the importance of salinity as an excluding axis in the distribution of some species of swimming crabs in the surf and estuarine pond of Ensenada de La Vela. In our study, *A. cribrarius* was present in salinities from 30‰ to 43‰, thus exceeding the upper limits of tolerance commonly reported for this species. The restricted distribution of this species is probably a consequence of its stenohalinity (27.5–36.5‰) (Gunter, 1950; Norse, 1978; Williams, 1984; Pinheiro, 1991; Avila and Branco, 1996), although very occasionally it may show up in estuaries (Williams, 1965) and can tolerate experimental salinities down to 17.25‰ (Norse, 1978). This range indicates that *A. cribrarius* prefers marine or near-marine environments, thus explaining its absence in station 3 (estuarine). In spite of being considered to be well adapted to heavy surf in shallow coastal waters (Fischer, 1978; Williams, 1984), *A. cribrarius* appeared to be abundant in all three foreshore stations, independent of water movement, and was most abundant in the more protected stations 1 and 2. Because the salinity did not show any major differences between foreshore and offshore habitats, other factors are at stake in determining the zonation observed for the other species. One of the main elements to consider is substrate composition (Norse and Fox-Norse, 1979; Pinheiro et al., 1997). Pinheiro et al. (1997) stated that distributional patterns of portunids in Fortaleza Bay (Brazil) are driven mainly by the granulometric composition of the sediments. Substrates at the foreshore and estuarine pond differed from offshore bottoms: at the foreshore the sediment was mainly sand; at the estuarine station a muddy bottom prevailed. At the offshore stations, silt was the main substrate. Hence, this difference could influence the distribution of swimming crabs in Ensenada de La Vela.

Callinectes danae was found in both biotopes at the foreshore but was more abundant at the estuarine site. In the marine stations of the surf zone, *C. danae* appeared more frequently in the most protected areas. The appearance and persistence of this species in both environments probably stems from its euryhalinity. In several Caribbean locations, *C. danae* has been observed dwelling in polyhaline environments (Taissoun, 1969; Norse, 1978; Buchanan and Stoner, 1988). Based on this evidence, it is not surprising to find *C. danae* in the entire range of salinities in Ensenada de La Vela, although it is important to underline that at the estuarine station it appeared when salinity was below the minimum (11‰) reported by Norse (1978). Also, several of the portunid species in the surf zone in Ensenada de La Vela were found in higher salinities than those reported by Norse (1978) in several localities in Jamaica, except *C. maracaiboensis* and *C. larvatus*. The absence of *C. ornatus* at the foreshore stations may be due to reasons other than the sampling method, because the same method was used by Carmona-Suárez and Conde (1996), where specimens of *C. ornatus* were frequently captured at different sites in the State of Falcón, Venezuela, including Ensenada de La Vela.

Total abundance of all swimming crabs both at the surf zone and at the estuarine station fluctuated widely and randomly through the year. This pattern also emerged when only the temporal abundance variations of the dominant species, *A. cribrarius* and *C. danae*, were examined. No significant correlations were found between abundances of these two species and rainfall, dissolved oxygen, water temperature, or salinity fluctuations. However, the inverse correlation of dissolved oxygen and abundance reached almost significant levels for both species at the marine foreshore and indeed was significant for the total abundance of crabs in the surf. Additionally, there was a positive correlation between rainfall and total abundance of crabs in the estuarine zone, possibly due to the increment of organic material washed into this environment from adjacent terrestrial areas. Although bibliographic evidence supports the adaptation of portunids to low levels of dissolved oxygen in their environment (DeFur et al., 1990; Rantin et al., 1996; Mangum, 1997), and the relation between respiration rates and salinity in two *Callinectes* species (Rosas et al., 1989), nothing supports the idea that the increase of swimming crab densities is due to the decrease in dissolved oxygen. It might be possible that augmenting food resources would increase populations of fishes and invertebrates

or planktonic blooms, which in turn would require a higher oxygen demand in the area, subsequently provoking drops in oxygen and causing mortalities of high-oxygen-demanding invertebrates. In any event, these results suggest that fluctuations in oxygen levels might be a key element in regulating portunid populations at Ensenada de La Vela and merit further research efforts.

Berried females were remarkably scarce during our study. Only two, both belonging to *C. danae,* were caught throughout the first period at the estuarine site, and none were caught during day and night samplings in the surf zone nor offshore. Nonetheless, scarcity of ovigerous females of swimming crabs in these coasts is not exceptional. During a 2-year survey of crustaceans along 700 km of Falcón's shoreline, Carmona-Suárez and Conde (1996) caught very few berried females of several of the littoral portunid species. They caught only one berried female of *A. cribrarius* and no ovigerous females of *C. sapidus*, *C. larvatus*, *C. ornatus*, or *C. danae*. However, in estuarine areas, substantial numbers of berried females of *C. bocourti*, *C. maracaiboensis,* and *C. exasperatus* were caught in the tidal zone. The scarcity or sheer absence of egg-bearing females in some species of swimming crabs might be the result of habitat partitioning by sex. Differential distributions by sex have been reported for *C. sapidus* (Williams, 1965; Perry, 1975; Archambault et al., 1990), *C. maracaiboensis* (Norse, 1977), and *C. bocourti* (Taissoun, 1969; Norse, 1978). However, for the dominant species in the surf, *A. cribrarius*, ovigerous females do not seem to be segregated into deeper waters. In southern Brazil, ovigerous females of this species appeared in shallow waters close to the coast (Pinheiro et al., 1996). Similarly, many ovigerous females were collected in very shallow water, at the surf's edge in North Carolina (Williams, 1984). Likewise, for *C. bocourti* and *C. maracaiboensis* egg-bearing females have also been reported in marine shallow waters (Norse, 1977). Furthermore, adult females of most species inhabiting the surf zone at Ensenada de La Vela were observed in this area year-round. Thus, alternative explanations should be considered, such as lack of estuarine habitats or sustained harsh environmental conditions that do not allow energy to be invested in reproduction. For instance, a highly seasonal reproductive pattern, with periods without berried females, has been observed in populations of the mangrove tree crab, *Aratus pisonii,* living in hypersaline lagoons in this area (Conde, 1989); this pattern contrasts with the pattern for populations inhabiting other localities, where these crabs reproduce continuously throughout the year (Conde and Díaz, 1989a; Díaz and Conde, 1989). Also, undergrown or stunted specimens of various species of crustaceans have been reported in this area (Conde and Díaz 1989b, 1992a, 1992b; Carmona, 1992; Carmona-Suárez and Conde, 1996). Thus, it is possible that this arid coast lacks the necessary resources for these crabs to reproduce, except in a few estuarine spots. This hypothesis is also supported by the fact that the body size of several species of swimming crabs collected in our study was smaller than that reported in other locations (Fischer, 1978; Williams, 1984).

The only river near the Ensenada de La Vela is the Coro River, which lies approximately 2 km westwards. Because of current direction (east–west), it cannot influence estuarine conditions to the sampled area. The small estuary in the Ensenada de la Vela could be a possible local nutrient supplier. But its influence is restricted to a few days during the end of each year, when the estuary opens to the sea. The setup of an untreated sewage discharge in the small estuarine basin at the beginning of 1997 could in fact have a long-term impact, but it is possible that various species of swimming crabs may not be affected negatively, because of their capacity to live in polluted areas. Such is the case with *C. bocourti* (Taissoun, 1972; Williams, 1974), and *C. sapidus*, the main species in the Lake Maracaibo crab industry (Oesterling and Petrocci, 1995), where contamination due to several sources (i.e. sewage and oil) has reached high levels (Rodríguez, 2000).

Because trawl studies have shown greater abundances of blue crabs (*C. sapidus*) and, in general, other decapods at night (Wilson et al., 1990), we ran a series of day and night samplings at the marine front over a six-month period and later also undertook diel offshore pot sampling on several occasions. Although Fischer (1978) has stated that *A. cribrarius* burrows into the bottom during the day and emerges at night, we collected *A. cribrarius* in the same range of abundances and sizes during both day and night samplings. Similar results were achieved by DeLancey (1989) in South Carolina, where no significant differences were obtained from samples collected at day and night. Wilson et al. (1990) ascribed the lack of differences in day and night abundances of *C. sapidus* to the use of more effective sampling devices than previously employed. In our study, no major differences were observed in diversity, abundance, body size, or sex ratios for most species, even though two kinds of collecting gears were used; thus, it is feasible to consider that if daily cycles exist in the species, they do not have a significant impact on daily density variations. In turn, these findings may have practical consequences for the decisions regarding sampling schemes to assess fisheries in this area.

The exploitation of swimming crabs at Ensenada de La Vela must be considered only at the artisanal level because of the low abundance of all species treated in our work and their wide and random density fluctuations. In fact, local fisheries are currently limited to the artisanal capture of portunids by hanging nets or hand-driven trawling nets. The most captured species by fishermen is *C. bocourti* (senior author, personal obs.), but *C. danae* is also a promising staple to be harvested because it appears in all three major biotopes (marine inshore, offshore, and estuarine). *Arenaeus cribrarius*, a species commercially exploited in Brazil (Pinheiro and Franzoso, 1998) and regarded to have an excellent flavor (Fischer, 1978), may also be considered a target species because of its great abundance, although its small size may make it less desirable commercially.

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Age, growth, and reproduction of permit (*Trachinotus falcatus*) in Florida waters

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Abstract–We examined 536 permit (*Trachinotus falcatus*, 65–916 mm FL) collected from the waters of Florida Keys and from the Tampa Bay area on Florida's Gulf coast to describe their growth and reproduction. Among permit that we sexed, females ranged from 266 to 916 mm in length (mean=617) and males ranged from 274 to 855 mm (mean=601). Ages of 297 permit ranging from 102 to 900 mm FL were estimated from thin-sectioned otoliths (sagittae). The large proportion of otoliths with an annulus on the margin and an otolith from an OTC-injected fish suggested that a single annulus was formed each year during late spring or early summer. Permit reach a maximum age of at least 23 years. Permit grew rapidly until an age of about five years, and then growth slowed considerably. Male and female von Bertalanffy growth models were not significantly different, and the sexes-combined growth model was $FL=753.1(1-e^{-0.418(t+0.585)})$. Gonad development was seasonal, and spawning occurred during late spring and summer over artificial and natural reefs at depths of 10–30 m. Ovaries that contained oocytes in the final stages of oocyte maturation or postovulatory follicles were found during May–July. We estimated that 50% of the females in the population had reached sexual maturity by 547 mm and an age of 3.1 years and that 50% of the males in the population had reached sexual maturity by 486 mm and an age of 2.3 years. Because Florida regulations restrict the maximum size of permit caught in recreational and commercial fisheries to 20-inch (508-mm), most fish harvested are sexually immature. With the current size selectivity of the fishery, the spawning stock biomass of permit could decrease quickly in response to moderate levels of fishing mortality; thus, the regulations in place in Florida to restrict harvest levels appear to be justified.

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The family Carangidae supports a diverse array of economically important fisheries in tropical and subtropical waters worldwide. In the southeastern United States, many carangid stocks are managed at both the state and Federal level. Recently, the National Marine Fisheries Service determined that the Gulf of Mexico greater amberjack stock is overfished, but the status of most carangid stocks is unknown (Anonymous[1]). For most carangid stocks, no quantitative stock assessments have been completed, in part, because little biological information exists regarding carangid growth rates and reproduction. As a result, the adequacy of current management measures to prevent overfishing of many carangid stocks is unclear.

Permit, *Trachinotus falcatus*, are the basis of an important recreational fishery and a small commercial fishery in Florida. Estimates of Florida recreational landings are unreliable but may exceed 100,000 fish per year (Armstrong et al.[2]). Commercial landings of permit peaked in 1991 at 200,000 pounds and then decreased to 50,000 pounds in 1995 (Armstrong et al.[2]). Current regulations in Florida include a 10-inch (254-mm FL) minimum size limit and a 20-inch (508-mm FL) maximum size limit on both the recreational and commercial harvest. In addition, recreational anglers are permitted daily to take 10 permit per bag of combined permit and Florida pompano (*Trachinotus carolinus*). Many anglers pursuing permit do so with professional guides on a charter vessel. In addition to being popular in South Florida, permit are targeted by numerous fishing tourists and recreational anglers in the Bahamas and at locations throughout the Caribbean. Despite the economic importance of permit in these regions, there are no published reports describing growth, longevity, or length and age at sexual maturity. Such information is needed to evaluate the effects of fishing mortality on permit populations. Previous studies of permit life history by Fields (1962) and Finucane (1969) were based only on an examination of larvae and young-of-the year permit. Our study describes growth, longevity, and the length and age at which fish become sexually mature. In addition, we document spawning of permit in South Florida waters based upon a histological examination of ovaries and seasonal patterns in the abundance of juveniles.

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Methods

Collections

Permit that we examined were collected from the Florida Keys (n=308; between 25°40′N, 80°10′W and 24°30′N, 82°20′W) during 1995–97 and the Tampa Bay area (n=228; 27°40′N, 82°45′W) during 1990–95. Most Florida Keys permit were caught with hook-and-line gear (n=215) or speared (n=58) over artificial and natural reefs in the waters off the lower and middle Keys in depths ranging from 10 to 30 m. Other, usually smaller, permit were captured with gill nets (n=16), seines (n=18), and bottom trawls (n=1) over or near shallow banks adjacent to the Keys. Most of the permit sampled in the Tampa Bay area were small (<400 mm FL) and were captured with seines along sandy beaches; some larger Tampa Bay permit were captured with gill nets (n=53) or trammel nets (n=14).

Standard length (SL), fork length (FL), and total length (TL) were measured to the nearest millimeter (mm) and weight was measured to the nearest gram. Unless otherwise indicated, all lengths reported in our study are fork lengths. Otoliths (sagittae) were removed, rinsed in water, and stored dry until sectioned; they were later weighed to the nearest 0.01 mg. Gonad weight was recorded to the nearest gram (g), and gonad samples were removed from the fish and preserved in 10% buffered formalin; they were later soaked in water for 24 hours and stored in 70% ethanol.

Collections of juvenile permit from sandy beaches off Tampa Bay and the Florida Keys were made with a 21.3 × 1.8-m bag seine (6.4-mm mesh in the wings and 3.2-mm mesh in the bag). Seine hauls were made perpendicular to the beach for distances up to 50 m, depending on water depth. Lengths of up to 50 fish from each sample collection were measured to the nearest millimeter. Near Tampa Bay, we collected fish at the Gulf of Mexico beaches of Treasure Island (November 1992 –October 1994; 27°46′N, 82°46.5′W) and Indian Shores (August 1993–November 1994; 27°50′N, 82°50′W). Sampling at each site consisted of five seine hauls every two weeks. Six sandy beaches were sampled monthly in the Florida Keys from July 1994 to July 1997: Lower Matecumbe Beach (July 1994–April 1996; 24°50.95′N, 80°4415′W), Coco Plum Beach (July 1994–April 1996; 24°43.65′N, 81°00.10′W), Clarence P. Higgs Beach, Key West (July 1994–July 1997; 24°32.79′N, 81°47.26′W), Bahia Honda State Park (October 1994–May 1997; 24°39.81′N, 81°15.44′W), Boca Chica Beach (October 1994–April 1996; 24°33.60′N, 81°41.65′W), and Sugarloaf Beach (January 1995–May 1996; 24°36.57′N, 81°33.49′W).

Age and growth

The left sagitta was usually used for age estimation; however, if the left otolith was broken, lost, or destroyed during processing, the right otolith was substituted. We prepared otoliths for age estimation by embedding them in Spurr, a high-density plastic medium (Secor et al., 1992). A 1-mm to 2-mm-thick transverse section containing the otolith core was cut with a Buehler Isomet low-speed saw with a diamond blade. The section was mounted on a microscope slide with thermoplastic glue (CrystalBond 509 adhesive) and was polished with wet or dry sandpaper (grit sizes ranging from 220–2000) until annuli were visible. Sections were then polished on a Buehler polishing cloth with 0.05-gamma alumina powder to remove scratches. Without knowledge of fish size or capture date and using a compound microscope equipped with transmitted light, two readers independently counted annuli on each otolith twice. If three of the four readings agreed, then this mode was accepted as the annulus count. If three of the four readings did not agree, each reader again counted annuli independently and without knowledge of previous counts. If three of the resulting six readings agreed, then this mode was accepted as the annulus count. If there were not three readings that agreed, the otolith was excluded from further analysis. In six cases, two sets of three readings that were in agreement occurred. For these six otoliths the two sets of readings differed by only one annulus; therefore the mean was accepted as the annulus count.

The percentage of otoliths with an annulus on the edge was then plotted by month so that we could look for a seasonal pattern in annulus formation. We did not attempt to measure marginal increments because the margin of permit otoliths is highly sculptured and easily broken; however, we did believe that we could discern the presence of an annulus on the otolith's edge.

The von Bertalanffy (1957) growth equation $FL_t = L_\infty (1-e^{-K(t-t_0)})$ was fitted to observed age-length data with nonlinear regression procedures. Age was esimated as the annulus count because permit both spawn and form annuli at about the same time of year. Our estimates of length at age include some seasonal growth that occurred after the formation of the final annulus. Length-weight regressions were calculated by linear regression of $\log_{10}$-transformed data.

Sex-specific growth models were compared with an approximate randomization test described by Helser (1996). This test is based on the premise that when the null hypothesis of no sex-specific differences in growth is true, a test statistic derived by random assignment of fish to one of two populations will not be different from that observed between sexes. The test statistic is calculated as the residual sums of squares for the sexes-combined von Bertalanffy growth model minus the residual sums of squares for the two sex-specific models. A probability distribution of the test statistic was generated by a randomization routine with 1000 iterations of the nonlinear models. Only sexed fish were included in the statistical comparison.

Age validation

Permit used in the age-validation experiments were captured in waters off the Florida Keys with hook-and-line gear. After capture, permit were tagged with dart-type tags and injected with Liquamycin LA-200 (200-mg oxytetracycline [OTC]/mL) in the dorsal musculature at a dosage of about 100-mg OTC per kg fish weight. Permit were then held in a 33.5-m-long by 5.5-m-wide by 0.75-m-

deep pond at the Florida Fish and Wildlife Conservation Commission's Keys Marine Laboratory in Long Key. Fish were held at ambient temperatures and were fed frozen shrimp and fish until satiated at least three times a week. Although several permit were injected and held for various periods, only one fish survived long enough to have formed an annulus after the OTC injection. The otolith section from this fish was examined with a compound microscope (40–100×) equipped with ultraviolet light so that the fluorescent OTC mark could be detected.

Reproduction

Histological sections of gonads were prepared and assessed for reproductive state. Gonad samples were prepared for histological examination with a modification of the periodic acid Schiff's (PAS) stain for glycol-methacrylate sections and with Weigert's iron-hematoxylin as a nuclear stain and metanil yellow as a counterstain (Quintero-Hunter et al., 1991).

Developmental stages of oocytes were determined and oocytes were counted from histological preparations at 100× with a compound microscope attached to a digital image-processing system. Four oocyte stages were recognized in permit ovaries: primary growth, cortical alveolar, vitellogenic, and oocytes in the final stages of maturation (Wallace and Selman, 1981). The final stages of oocyte maturation (FOM) included yolk coalescence, germinal vesicle migration, germinal vesicle breakdown, and hydration. We also counted postovulatory follicles (POFs) and PAS-positive melanomacrophage centers (Ravaglia and Maggese, 1995; Crabtree et al., 1997), which were present in many ovaries. When stained with the PAS stain, these PAS-positive structures are brilliant purple. Melanomacrophage centers are thought to be active in degrading atretic oocytes, postovulatory follicles, and residual cells of the spermatogenic cycle (Chan et al., 1967; Ravaglia and Maggese, 1995). The developmental stage of at least 300 oocytes and other structures on each slide was determined and counted in arbitrarily chosen fields, and frequencies were expressed as a percentage of the total count. We counted all oocytes that had at least 50% of their area visible in a field before moving to the next field.

We examined seasonal reproductive patterns by plotting monthly juvenile length frequencies and monthly mean gonadosomatic indices (GSIs). Gonadosomatic indices were calculated for 129 sexually mature female permit ranging in length from 476 to 916 mm and for 122 sexually mature male permit ranging in length from 449 to 855 mm as

$$GSI = (GW / (TW - GW))100,$$

where GW = total gonad weight (g); and
TW = total fish weight (g).

Length and age at sexual maturity

Females were considered sexually mature if vitellogenic oocytes were present or if the histological sections appeared disorganized, highly vascularized, and contained widespread evidence of atresia. We followed the classification of Hunter and Macewicz (1985) in recognizing atresia. Most immature females had small well-organized gonads that contained little evidence of atresia. We interpreted the widespread occurrence of PAS-positive melanomacrophage centers in inactive ovaries as evidence of past gonadal development, and we considered permit with regressed (no vitellogenic oocytes present) ovaries that contained many of these structures to be sexually mature. Males were considered sexually mature if testes contained evidence of ongoing spermatogenesis, residual sperm, or widespread PAS-positive melanomacrophage centers associated with gonadal recrudescence. We estimated the length and age at which 50% of the fish in the population reached sexual maturity by fitting a logistic function to the percentage of fish that were sexually mature and to their respective lengths and ages. Regressions were performed with sex as a categorical effect. If sex was a significant effect, the equations were then reduced to separate sex-specific equations. The inflection point of the logistic curves was used as an estimate of the length or age at which 50% of the population had reached sexual maturity.

Results

Permit that we collected from waters off the Florida Keys ranged from 258 to 916 mm in length (n=308), and the permit collected from the Tampa Bay area ranged from 65 to 812 mm in length (n=228). Among permit that we sexed, females ranged from 266 to 916 mm in length (mean=617, SD=155.7, n=187) and males ranged from 274 to 855 mm (mean=601, SD=145.8, n=166; Fig. 1). The sex ratio of our sample was 1:1.1 (male:female) and was not significantly different from 1:1 (χ^2 test, P>0.05). Neither the slopes (P=0.464) nor the elevations (P=0.063) of the length-weight equations for male and female permit were significantly different. The pooled length-weight equation for sexed and unsexed fish was

$$\log_{10} WT = 2.803 \log_{10} FL - 4.078, \qquad (n=488, r^2=0.996)$$

where WT = weight in grams; and
FL = fork length in mm.

Age and growth

When viewed with transmitted light, permit otoliths have opaque (dark) annuli that alternate with translucent (light) zones (Fig. 2). Proceeding from the otolith's core towards the otolith's proximal margin, annuli are regularly spaced along the sulcal ridge. In some individuals, the annuli are indistinct and irregular in appearance, which made age estimation difficult. We considered 51 otoliths (17.3%) from permit ranging in length from 243 to 916 mm to be unreadable. The length-frequency distribution of fish whose otoliths were considered unreadable was not significantly different from that of fish whose otoliths were considered readable (Kolmogorov-Smirnov two-sample test, D=0.144, P=0.32); thus, no particular length

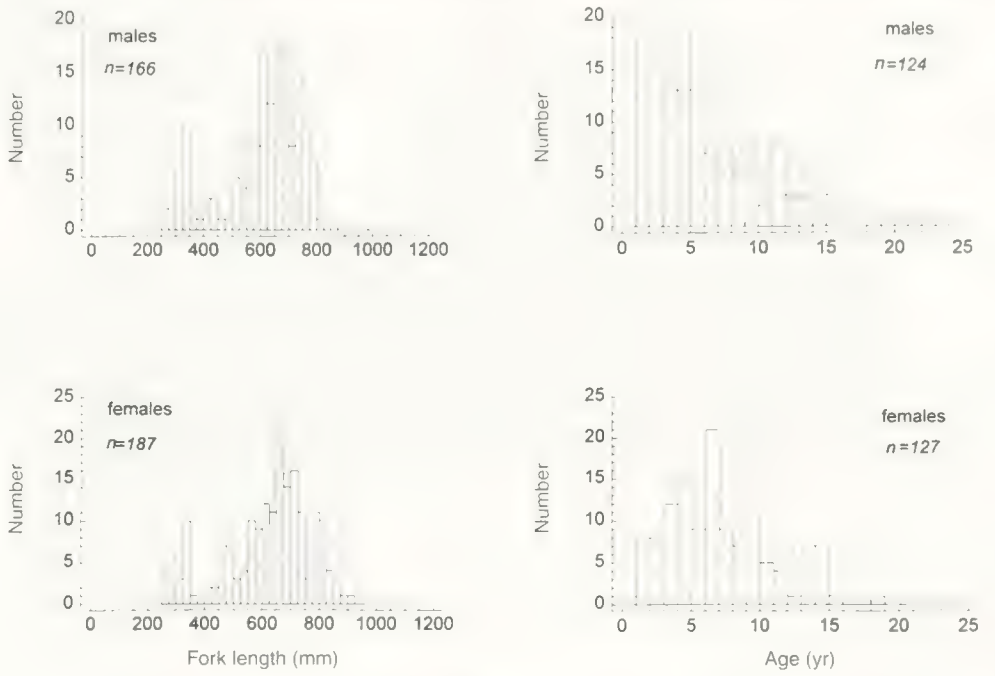

Figure 1

Fork lengths (mm) and ages (years) of male and female permit, *Trachinotus falcatus*, sampled from South Florida waters.

group of fish was systematically excluded from the age-and-growth analysis.

Annulus formation in permit occurs during spring and early summer. The percentage of permit with an annulus on the otolith's margin was greatest during summer and least during October–March, suggesting that annulus formation is seasonal and that annuli first become visible during late spring or early summer (Fig. 3). A single OTC-injected permit was successfully held for a sufficient length of time to be useful in age validation. This fish was captured and injected with OTC on 17 June 1993. The fish was sacrificed on 30 January 1996 and measured 600 mm in length. After 31 months in captivity, which included two spring-summer periods, the fish had formed two annuli, a number that is consistent with our hypothesis that a single annual mark forms annually during late spring or early summer. Also visible immediately before the OTC mark was an annulus that was probably formed during late spring of 1993, just prior to capture and OTC injection. Moreover, there was a wide margin subsequent to the last annulus that is consistent with the six or more months of otolith growth after formation of the final annulus in late spring or early summer of 1995.

Estimated ages of 298 permit ranged from 0 to 23 years for fish 102 to 900 mm long. Permit grew rapidly until about age five, and then growth slowed considerably (Table 1, Fig. 4). Most of the fish in our sample were less than 10 years old, although fish 10–15 years old were common. The oldest permit examined was a 23-year-old (781-mm) male (Table 1). Estimates of von Bertalanffy growth model parameters are presented in Table 2. The growth models for male and female permit were not significantly different (approximate randomization test, P=0.059).

Sexual maturation

We estimated that 50% of the males in the population reached sexual maturity by 486 mm and an age of 2.3 years, and 50% of the females in the population reached sexual maturity by 547 mm and an age of 3.1 years (Table 3). The smallest sexually mature male in our sample was 449 mm long, and the youngest sexually mature male was 3 years old. Our estimate of the age at 50% maturity for males was less than the age of the youngest mature male observed. This knife-edge maturity curve could be an artifact of our small sample size. The smallest sexually mature female in our sample was 476 mm long, and the youngest sexually mature female was 3 years old. All of the ovaries we examined contained primary-growth-stage oocytes. Cortical alveolar-stage oocytes occurred only in ovaries from permit larger than 450 mm and older than 2 years and were common only among permit larger than 500 mm and older than 3 years. Vitellogenic oocytes were found only in ovaries from fish larger than 550 mm and older than 3 years and were common only among permit larger than 600 mm. The length and age at which vitellogenic oocytes were commonly found agrees well with our estimate of the length and age at which 50% maturity was

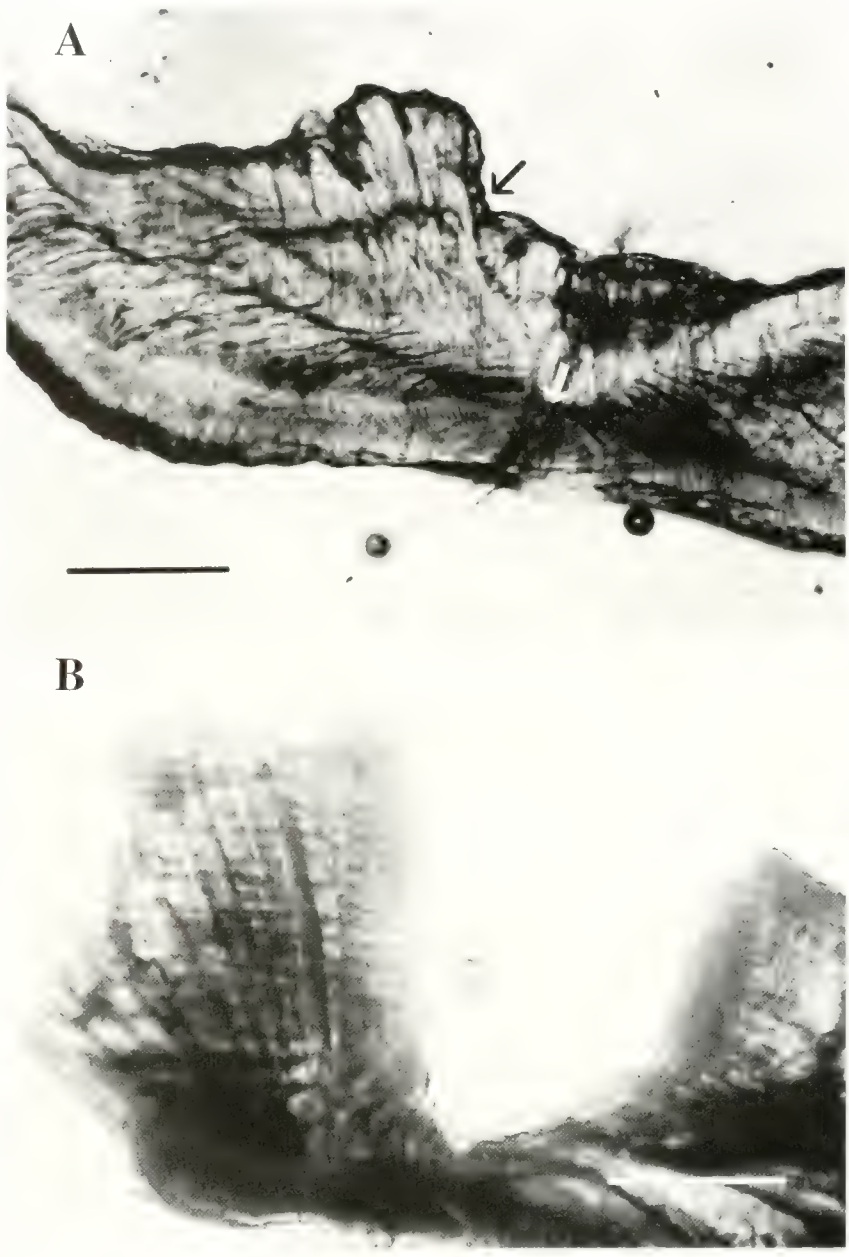

Figure 2

(**A**) Sectioned sagitta from a 1-year-old (363-mm-FL) permit, *Trachinotus falcatus*, collected in the Florida Keys on 27 February 1995, showing the location of the core (white arrow) and the first annulus (black arrow). Scale bar = 200 microns. (**B**) Sectioned sagitta from a 23-year-old male permit (781-mm-FL) collected in the Florida Keys on 4 June 1996. Scale bar = 500 m.

reached, suggesting that we misclassified few gonads with regression.

Spawning seasonality

Permit spawning appeared to be seasonal in the areas we sampled and occurred at least during May–July. We examined 15 permit ovaries that contained either oocytes in the final stages of maturation or POFs, structures indicative of imminent or recent (<24 h) spawning. We usually did not know the time of day when fish were caught, but all fish were captured during daylight hours (0700–1700 h). Oocytes in the final stages of maturation were found during June and July, and POFs were found

Table 1

Average observed and predicted fork lengths (mm) of permit, *Trachinotus falcatus*. The average observed length at age includes some seasonal growth that occurred after the formation of the final annulus. Values in parentheses are standard error and sample size.

	Sexes combined		Females		Males	
Age (yr)	Average observed	Predicted	Average observed	Predicted	Average observed	Predicted
0	160 (12.7;17)	139	277 (1)	212		149
1	301 (5.9;56)	319	310 (14.5;8)	353	334 (12.5;17)	337
2	476 (7.6;10)	447	479 (6.8; 8)	458	465 (33.5;2)	464
3	564 (10.1;27)	537	555 (12.1;13)	538	572 (15.9;14)	550
4	612 (6.3;28)	601	620 (9.8;14)	599	604 (7.6;14)	608
5	643 (8.7;29)	645	664 (13.8;10)	644	632 (10.5;19)	647
6	663 (8.7;26)	677	658 (10.7;20)	679	680 (9.3;6)	673
7	687 (12.0;17)	699	687 (10.8;9)	704	687 (23.6;8)	691
8	703 (16.9;12)	715	695 (22.7;7)	724	715 (27.4;5)	703
9	713 (15.1;21)	726	710 (26.8,11)	743	717 (13.3;10)	711
10	743 (30.0;6)	734	754 (34.2;5)	750	688 (1)	717
11	746 (21.8;12)	740	811 (25.3;4)	758	714 (23.2;8)	721
12	738 (35.3;5)	744	797 (0.5;2)	765	698 (46.9;3)	723
13	787 (19.4;9)	746	803 (26.2;6)	769	754 (15.7;3)	725
14	762 (19.5;13)	748	783 (12.8;7)	773	737 (38.9;6)	726
15	753 (13.4;4)	750	737 (1)	776	759 (17.3;3)	727
16		751		778		727
17		751		779		727
18	745 (48.5;2)	752	793 (1)	781	696 (1)	728
19		752		781		728
20	667 (1)	753	782		667 (1)	728
21	687 (1)	753	916 (1)	783	687 (1)	728
22		753		783		728
23	781 (1)	753	783		781 (1)	728

Table 2

Parameter estimates of the von Bertalanffy growth model for permit, *Trachinotus falcatus*, from South Florida waters. Values in parentheses are standard errors. FL = fork length.

Sex	n	L (mm FL)	K	t_0	adjusted r^2
Females	127	784.2 (13.79)	0.28 (0.027)	–1.12 (0.249)	0.833
Males	123	728.2 (9.52)	0.39 (0.034)	–0.58 (0.168)	0.855
Combined	297	753.1 (7.12)	0.35 (0.015)	–0.59 (0.065)	0.921

during May–July (Fig 5). Vitellogenic oocytes were most plentiful during March–July and were absent during October–December. No samples were available for histological examination in January or February, but it seems

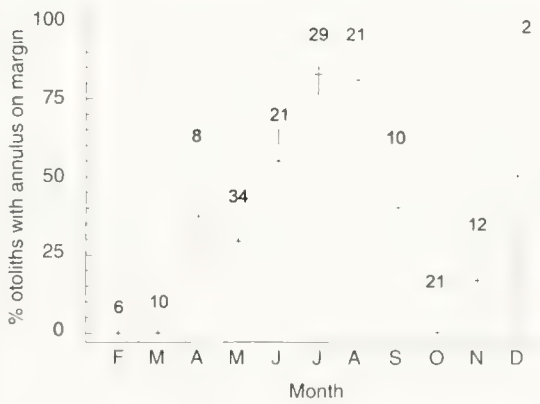

Figure 3

Mean percentage and standard error of permit (*Trachinotus falcatus*) otoliths with an annulus on the margin plotted by month. Numbers above the lines are the monthly sample sizes.

unlikely that spawning occurred during these months. Females with the greatest GSIs (>4%) were captured during March–August, and GSIs were least (<1.5%) during October–December (Fig. 6). Male GSIs were generally similar in magnitude to female GSIs and followed the same pattern.

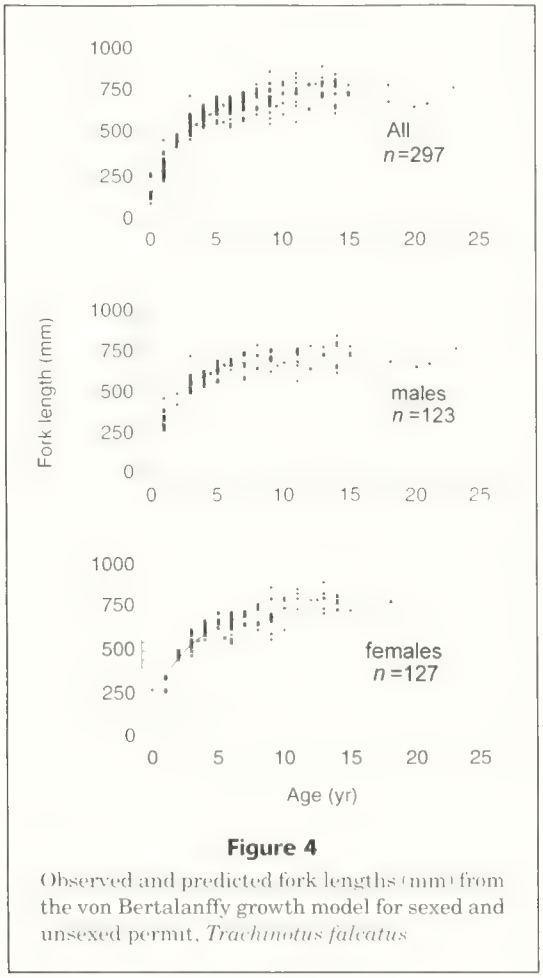

Figure 4

Observed and predicted fork lengths (mm) from the von Bertalanffy growth model for sexed and unsexed permit, *Trachinotus falcatus*

In the Tampa Bay area, small permit (<40 mm) were present from June to November, suggesting that spawning extends into the fall. In the Florida Keys, small fish (<40 mm) were present all year, suggesting an extended spawning season, recruitment from other areas with different seasonal spawning patterns, or variable juvenile growth rates.

Discussion

We obtained permit from a variety of fishery-dependent and fishery-independent sources; consequently, our sample is biased towards certain size classes, and the bimodal size-frequency distribution of our sample probably does not reflect that of the population or the Florida harvest. All the small fish (<300 mm) we examined were from fishery-independent sources; most large fish were from fishery-depen-

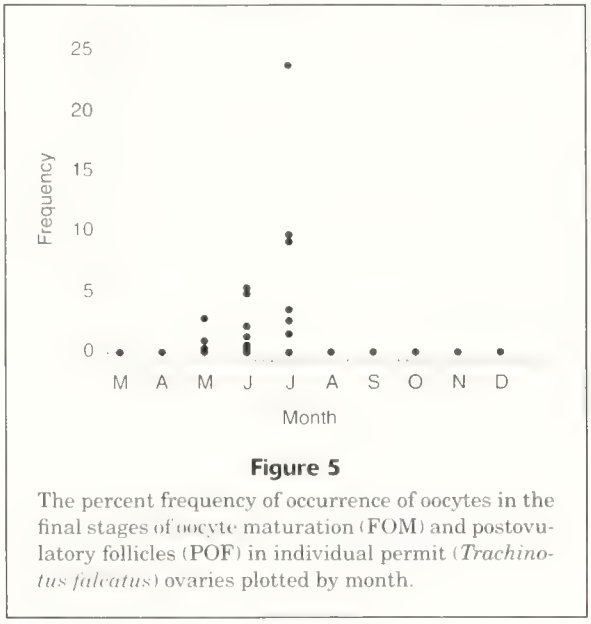

Figure 5

The percent frequency of occurrence of oocytes in the final stages of oocyte maturation (FOM) and postovulatory follicles (POF) in individual permit (*Trachinotus falcatus*) ovaries plotted by month.

Table 3

The relationship of percentage mature and fork length (mm) and the relationship of percentage mature and age (years) for permit, *Trachinotus falcatus*, from South Florida waters. *FL* = fork length (mm) and *AGE* = age (years). P_{50} is the absolute value of $((a+b)/c)$, is the inflection point of the curve, and is the length or age predicted by the logistic regression at which 50% of the permit in our sample were sexually mature. Sex is a dummy variable equal to 1 for males and 0 for females. PD is the adjusted percentage of deviance explained by the model.

		Percent female = $e^{(a+b(\ldots)+c(\ldots))}/(1+e^{(a+b(\ldots)+c(\ldots))})$				
X	*n*	*a*	*b*	*c*	PD	P_{50}
FL	314	–30.41	3.34	0.056	0.84	486 mm (males)
		(6.336)	(1.087)	(0.0114)		547 mm (females)
AGE	233	–6.71	1.71	2.14	0.09	2.3 years (males)
		(0.878)	(0.576)	(0.238)		3.1 years (females)

dent sources, such as charterboats. We did not sample any permit from the commercial fishery, which principally targets smaller fish as a result of the maximum size limit of 20 inches (508 mm FL) for permit caught by commercial vessels. Armstrong et al.[2] reported that most harvested permit in Florida were <440 mm. In contrast, our sample contained many fish larger than 600 mm. The high proportion of large permit in our sample could reflect a tendency for charterboats in the Florida Keys to select larger permit than those selected by more typical anglers statewide. Armstrong et al.'s[2] assessment was based on more systematic and statewide sampling than ours, and the differences between their sample and ours probably reflects our attempt to obtain a sample of all available size classes rather than a representative sample of the Florida harvest.

Age and growth

The oldest permit in our sample was estimated to be 23 years old. Although we examined many relatively large permit, larger fish than those we examined have been caught. Robins (1992) reported that permit can reach 1100 mm FL and a weight of 23 kg; consequently, permit longevity probably exceeds our estimate of 23 years. There are no other estimates of age and growth of permit for comparison, but our longevity estimates are similar to those determined from sectioned otoliths for other carangids. Manooch and Potts (1997) aged greater amberjack and found fish as old as 17 years. The oldest carangid yet studied is the trevally, *Caranx georgianus*, reported to reach an age of 46 years (James, 1984). The much smaller Florida pompano has been reported to reach an age of 7 years (Hood et al.[3]).

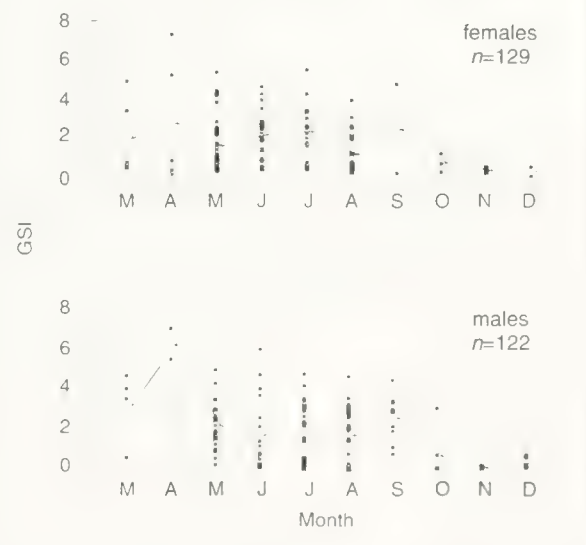

Figure 6

Gonadosomatic indices (GSI, •) and means (+) for sexually mature female and male permit, *Trachinotus falcatus*, plotted by month.

Our estimates of the von Bertalanffy growth model parameters are within the range of those reported for other carangids (James, 1984; Sudekum et al., 1991; Manooch and Potts, 1997). We found no significant differences between male and female von Bertalanffy growth models, but the significance level (P=0.059) was close enough to 0.05 to cause us to suspect that a difference might exist. Hood et al.[3] also found no sex-specific differences in growth models for pompano.

Sexual maturation

We sampled relatively few permit between 300 and 500 mm long, the size at which sexual maturity is reached. The lack of fish in this critical size range resulted in the knife-edge maturity curves. Larger sample sizes are needed to derive more precise estimates of age and size at sexual maturity. In an assessment of the status of permit stocks in Florida, Armstrong et al.[2] assumed that permit mature at about 440 mm FL on the basis of limited biological data available at the time. Our estimates of length at 50% maturity are larger: 486 mm for males and 547 mm for females. As a consequence of Florida's 20-inch (508-mm) recreational and commercial maximum size limit, most of the permit harvested are sexually immature (Armstrong et al.[2]).

Spawning

We believe that permit spawn over artificial and natural reefs in the waters of the middle and lower Florida Keys because ovaries of fish caught over these structures contained oocytes in the final stages of maturation and POFs. Other researchers have inferred that permit spawn in nearshore waters from the capture of early-stage larvae (Fields, 1962; Finucane, 1969). Permit ovaries that contained fresh POFs and oocytes in the final stages of maturation also contained clutches of early- and mid-stage vitellogenic oocytes, suggesting that permit are multiple-batch spawners.

Spawning occurred at least during May–June in the Florida Keys during 1995–97. Juvenile length frequencies in the Keys suggest a more prolonged spawning season—perhaps even year-round spawning; however, the prolonged presence of small juveniles could also be attributed to variable juvenile growth rates rather than extended spawning. This question could be resolved by direct aging of juveniles to evaluate growth rates. Our sample of adult permit may have been too small to reveal low levels of spawning outside of spring and early summer, and no mature permit were collected during January or February. On the basis of seasonal occurrence of juveniles, Finucane (1969) suggested that permit spawn during April–June in the Tampa Bay area, but Fields (1962) found juveniles

[3] Hood, P. B., D. T. Merryman, and D. J. Harshany. 1999. Age, growth, mortality, and reproduction of the Florida pompano, *Trachinotus carolinus*, from Florida waters. Unpubl. manuscript. Florida Marine Research Institute, 100 Eighth Avenue SE, St. Petersburg, FL.

year round suggesting a prolonged spawning period. Other carangids spawn during spring and summer: *Caranx ignobilis* and *Caranx melampygus* spawn during May–August in Hawaii (Sudekum et al., 1991) and *T. carolinus* spawns during January–August in Florida (Hood et al.[3]).

Our data suggest that maturation occurs at greater lengths than assumed by Armstrong et al.[2]; however, even using our maturation data, their observation that most permit landed are sexually immature remains true. With the current selectivity of the fishery, permit spawning stock biomass could decrease quickly in response to moderate levels of fishing mortality; thus, the regulations in place in Florida to restrict harvest levels appear to be justified. Significantly better estimates of the magnitude and age structure of the catch would be required to complete a comprehensive age-structured stock assessment.

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Tag-reporting levels for red drum (*Sciaenops ocellatus*) caught by anglers in South Carolina and Georgia estuaries*

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Abstract—A total of 1784 legal-size (≥356 mm TL) hatchery-produced red drum (*Sciaenops ocellatus*) were tagged and released to estimate tag-reporting levels of recreational anglers in South Carolina (SC) and Georgia (GA). Twelve groups of legal-size fish (~150 fish/group) were released. Half of the fish of each group were tagged with an external tag with the message "reward" and the other half of the fish were implanted with tags with the message "$100 reward." These fish were released into two estuaries in each state (n=4); three replicate groups were released at different sites within each estuary (n=12). From results obtained in previous tag return experiments conducted by wildlife and fisheries biologists, it was hypothesized that reporting would be maximized at a reward level of $100/tag. Reporting level for the "reward" tags was estimated by dividing the number of "reward" tags returned by the number of "$100 reward" tags returned. The cumulative return level for both tag messages was 22.7 (±1.9)% in SC and 25.8 (±4.1)% in GA. These return levels were typical of those recorded by other red drum tagging programs in the region. Return data were partitioned according to verbal survey information obtained from anglers who reported tagged fish. Based on this partitioned data set, 14.3 (±2.1)% of "reward" tags were returned in SC, and 25.5 (±2.3)% of "$100 reward" tags were returned. This finding indicates that only 56.7% of the fish captured with "reward" tags were reported in SC. The pattern was similar for GA where 19.1 (±10.6)% of "reward" message tags were returned as compared with 30.1 (±15.6)% for "$100 reward" message tags. This difference yielded a reporting level of 63% for "reward" tags in GA. Currently, 50% is used as the estimate for the angler reporting level in population models for red drum and a number of other coastal finfish species in the South Atlantic region of the United States. Based on results of our study, the commonly used reporting estimate may result in an overestimate of angler exploitation for red drum.

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Fish. Bull. 100:35–41 (2002).

There are major marine recreational fisheries along the south Atlantic and Gulf of Mexico coasts of the United States that target red drum, *Sciaenops ocellatus* (Matlock, 1986a; 1986b). During the late 1980s, overexploitation of red drum in many states resulted in the closure of commercial fisheries in most states and in the imposition of creel and size limits on catch of recreational anglers (McGurrin[1]) Concurrently, studies were initiated in a number of coastal states to gain a better understanding of red drum life history and to attempt to estimate exploitation rates. These investigations relied heavily on the use of fishery-dependent, mark-recapture studies to obtain the data necessary for creating a robust population model (McGurrin[1]).

Generic population models have been developed by using mark-recapture studies to estimate expected number of animals that survive and are recaptured from a year class within a given year (Brownie et al., 1985). Pollock et al. (1991) emphasized the need to modify tag recovery models in which data from multiyear tagging studies were used and suggested incorporating variables for postmarking survival and for reporting to estimate the recapture component of the model more accurately. The current model used to estimate recovery (recapture) rates of tagged fish (θ) includes a number of variables in an attempt to accurately account for what happens in nature ($\theta=\phi\mu\lambda$), where ϕ = tag retention multiplied by fish survival after tagging; μ = exploitation rate; and λ = reporting level (Hoenig et al., 1998). Reporting level (λ) of tagged fish captured by anglers is perhaps the most difficult variable to estimate accurately and is often assumed to be constant over time and geographic area (Hoenig et al., 1998).

* Contribution 467 of the South Carolina Department of Natural Resources, Charleston, South Carolina 29422-2559.

[1] McGurrin J. 1991. Fisheries management report 19 of the Atlantic States Marine Fisheries Commission. Fishery management plan for red drum—amendment 1, 123 p. Atlantic States Marine Fisheries Commission, 1400 16th St. NW Suite 310, Washington, D.C. 20036.

If the level of reporting can be closely estimated, then this estimated value can be incorporated into models that more accurately estimate survival and escapement (Hoenig et al., 1998).

In the past, researchers have attempted to accurately estimate reporting for marked animals in a number of ways. Some resource agencies have had creel clerks secretly implant tags into recreational anglers' creel during interviews, and others have conducted formal reward studies. For example, in Texas (TX), recreational anglers reported only 28% of a number of species of estuarine and marine finfish surreptitiously tagged by creel clerks (Matlock, 1981). A small-scale study during which red drum were surreptitiously tagged in Georgia (GA) also revealed low reporting levels (55%)(Woodward[2]). The GA study also noted trends in reporting by county and income level; however, because the number of tagged fish and subsequent returns in this study were small, valid statistical comparisons could not be made (Woodward[2]). Rawstron (1971) in a similar, more robust investigation conducted in freshwater lakes, found reporting levels of 50% for tagged bluegill, largemouth bass, and catfish and concluded that reporting appeared to be site and species specific.

Cash reward values ≤$50 have been used by many tagging programs to assess reporting levels (Rawstron, 1971; Matlock, 1981; Murphy and Taylor, 1991). In most cases, results have suggested that small cash awards do not provide adequate incentive for anglers to report capture of a tagged fish (Rawstron, 1971; Matlock, 1981; Murphy and Taylor, 1991). Work in California with stocked trout showed significantly higher reporting when a reward was offered, rather than no reward (Butler, 1962). Butler concluded that variability in reporting was also related to a number of other factors, including degree of publicity, angler interest in the fishery, and effort made to recover tags. Difficulty in determining reporting is not unique to fisheries population modeling. Historically, bands have been used to monitor populations of waterfowl and other birds. Reporting of banded waterfowl has also been shown to differ between locations (Henny and Burnham, 1976; Conroy and Blandin, 1984). For example, in areas where merchandise was regularly offered for banded birds, reporting decreased as compared with areas where capture of a marked bird was simply a novelty (Conroy and Blandin, 1984). Reward studies have attempted to overcome these problems by offering higher monetary rewards. In a study with waterfowl where rewards ranged from $5 to $1000, Nichols et al. (1991) demonstrated that there was a correlation between reporting and reward value. They also determined the asymptote for 100% reporting by duck hunters occurred between a reward value of $75 and $100. In a study of red drum in South Carolina (SC), Jenkins et al. (2000) found that $50 was not a high enough value to result in reporting differences between the standard "reward" message and a "$50 reward" message.

[2] Woodward, A. G. 1992. Evaluation of fish tag reporting by marine boat anglers in Georgia, 12 p. Georgia Department of Natural Resources, Coastal Resources Division, 1 Conservation Way, Brunswick, GA 31523.

For modeling purposes fishery managers in the south Atlantic region of the United States use reporting estimates of ~50% when analyzing return data for red drum. This approximate figure is used even though previous studies have shown that a number of variables may affect the accuracy of reporting tagged animals (Butler, 1962; Rawstron, 1971; Nichols et al., 1991; Ross et al., 1995; Woodward[2]). Assigning an approximate reporting level for the entire region could introduce bias in estimates of exploitation and potentially lead to significant exploitation of the population being managed. In previous studies where reporting levels for red drum and other finfish species were examined, there were a limited number of experimental units, making robust statistical analyses of the data difficult (Murphy and Taylor, 1991; Woodward[2]). This shortcoming is primarily due to logistical problems associated with capture, tagging, and release of sufficient numbers of similar-size wild fish in a manner that will ensure equal vulnerability to anglers over a large area (Yeager and Van Den Avyle, 1979; Murphy and Taylor, 1991). Our study attempts to reduce these problems by using similar-size hatchery-produced fish to carry tags. This experimental model allows a high degree of control over the design and implementation of a study (Jenkins et al., 2000). Further, fish can be tagged and stocked during seasons of the year when angler pressure is high, thereby minimizing the time required for data acquisition, as well as reducing variability associated with seasonal fluctuations in fishing effort (Jenkins et al., 2000). To assess the veracity of the currently used reporting estimate, a study was conducted in two estuaries in SC and two in GA. It was expected that the information obtained would provide a more accurate estimate for use in modeling red drum population dynamics in the south Atlantic region.

Materials and methods

All fish used in our study were progeny of locally captured wild broodstock. Adults had been spawned in tanks by using photoperiod and thermal conditioning (Roberts et al., 1978) at the SC Department of Natural Resources (SCDNR), Marine Resources Research Institute (MRRI) in Charleston, SC. Three day-old larvae were stocked in ponds at the SCDNR's Waddell Mariculture Center (WMC) in Bluffton, SC. When fish had grown to a mean total length (TL) of 200 mm, they were harvested and transported to MRRI. At MRRI, fish were grown to legal size (356 mm TL) in 4-m diameter tanks.

When fish were legal size (or approximately legal size), they were anesthetized in groups in a 0.1-g/L solution of MS-222 and culture water. Fish were then individually measured to the nearest mm and tagged with abdominal anchor tags (Floy Tag and MFG Co., Inc., Seattle, WA). In an effort to obtain results consistent with those from ongoing mark recapture programs in each state, fishery biologists from SC and GA tagged the fish to be stocked in their respective state. In addition, the tags used were identical to those used in ongoing studies in each state. For SC releases Floy model FM-95W tags were used.

These tags were completely orange and consisted of two parts: a 6.4-mm × 25.4-mm laminated disk wired to a 75-mm laminated streamer. The streamer portion contained the words "tag inside," a tag number, name of agency, and the reward message ("reward" or "$100 reward"). The disk portion contained the return address, reward message, a unique tag number, and the following: "reward, send tag, date, location, gear, length, phone number to ...". Tags used in GA tags were also Floy tags (model FM-89SL). As in SC, the tag consisted of two parts. The laminated disk was slightly smaller (6.4 mm × 19 mm) and yellow, whereas the streamer was the same length (75 mm) and was the same color (orange) used for fish released in SC. The streamer did not contain the words "tag inside" but it did contain the rest of the information found on the SC streamers plus "return to...". The disk portion contained much of the same information found on the SC disk except "reward, send tag, date, location, gear, length, phone number to ...". One half of the tags deployed in each state contained the message "$100 reward"; the remainder contained the message "reward." The "reward" message is the standard message that has been used for over 10 years in red drum mark-recapture studies in each state. Because of limitations in project funding and duration, the "$100 reward" tags also had an expiration date; "reward" tags, however, did not have an expiration date.

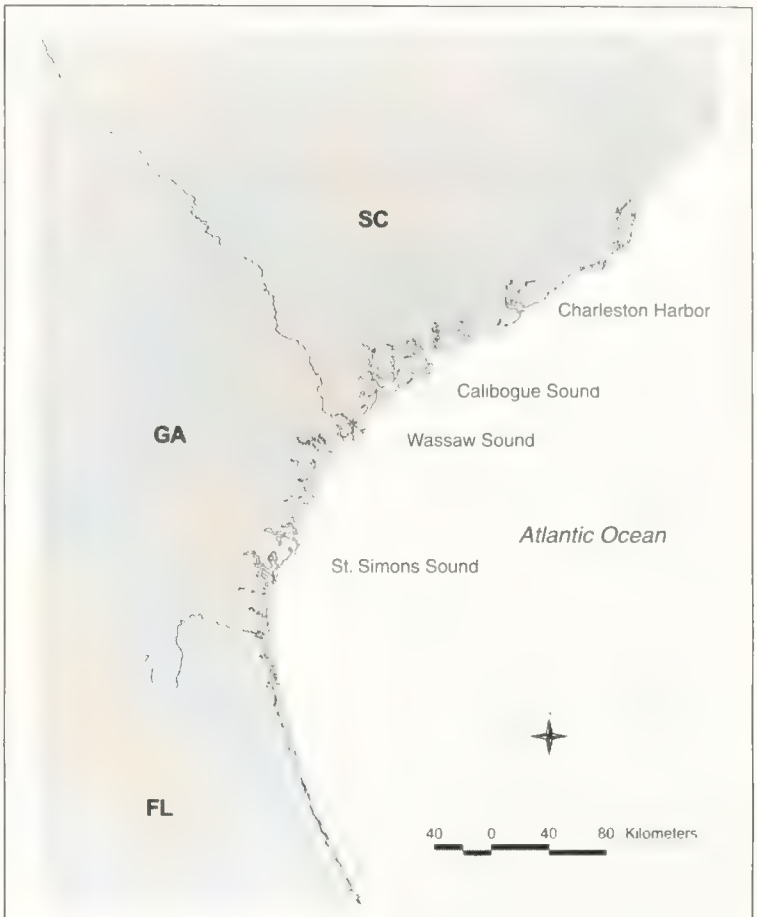

Figure 1

Map of coastal South Carolina (SC), Georgia (GA), and north Florida (FL) showing the location of each estuary where tagged red drum were released during the reward study.

After having been tagged, fish were retained in culture tanks for a minimum of one week to recover from handling. In preparation for release, marked fish were removed from the tanks and transported in oxygenated water, at a biomass density of ≤50 g/L, to the preselected estuaries. The estuaries in each state were as follows: Charleston Harbor and Calibogue Sound in SC; St. Simons Sound and Wassaw Sound in GA (Fig. 1). Three replicate release sites within each estuary were stocked with tagged fish. Upon arrival at each estuary, fish were acclimated for 1 hour to ambient water conditions prior to being transferred to holding tanks in boats. Within each estuary, the selected stocking sites had similar habitat characteristics and were geographically separate (≥5 km). At each site, fish were released individually approximately every 20 meters along the edge of the salt marsh to minimize the possibility of schooling behavior and subsequent multiple captures by individual anglers.

A total of 1774 fish were tagged and released during the project. Approximately 150 fish were released at each stocking site within each estuary (Table 1). Equal numbers of fish released at each site contained "reward" or "$100 reward" tags. Fish were released into Charleston Harbor, SC, and St Simons Sound, GA, during the fall of 1996 and into Calibogue Sound, SC, and Wassaw Sound, GA, during late spring and early summer 1997 (Table 1, Fig. 1). The expiration date for "$100 reward" tags deployed in fall 1996 was 31 March 1997, and for spring and summer 1997 releases, the expiration date was 31 December 1997. Neither the study nor the releases were publicized in any way other than by the normal information provided by ongoing tagging programs in each state. Captured tagged fish were reported directly to the respective Department of Natural Resources in each state. Participants who returned tags inscribed with "reward" received a prize that would normally be awarded by each agency (e.g. T-shirt or hat) and those reporting a "$100 reward" tag received a state-issued check for that amount.

Our study was based on two assumptions: 1) $100 was an adequate incentive to maximize reporting (assumed ~100%) of captured tagged fish; 2) the quotient of returns (the number of "reward"-inscribed tags divided by the returns of "$100 reward" tags) would yield the angler reporting level (λ) for the standard "reward" tag. Tags were returned in either of two ways: phone message or mail. All anglers who reported tags were later interviewed. During the interviews respondents were asked to confirm their reporting information and to express their attitudes and

Table 1

Cumulative data on release locations and stocking dates for fish, and both number of tags released and returned for each reward message.

		Tag			
		"Reward"		"$100 reward"	
Release location	Stocking date	No. released	No. returned	No. released	No. returned
Charleston Harbor					
site 1	31 Oct 1996	75	16	75	21
site 2	31 Oct 1996	75	18	75	21
site 3	31 Oct 1996	75	18	75	16
St. Simons Sound					
site 1	13 Nov 1996	75	10	75	17
site 2	13 Nov 1996	74	11	74	11
site 3	13 Nov 1996	75	10	75	15
Wassaw Sound					
site 1	8 May 1997	73	31	73	42
site 2	8 May 1997	75	23	75	29
site 3	8 May 1997	68	10	68	18
Calibogue Sound					
site 1	5 Jun 1997	75	9	75	21
site 2	9 Jul 1997	73	19	73	23
site 3	10 Jul 1997	74	9	74	12

opinions about the reporting procedure. All participants were asked the same questions from a standardized survey script. During the interview no information was provided to the anglers about the study design.

For statistical analysis each release site was treated as a replicate. By nesting site within estuary, within state, differences associated with each site, estuary, and state could be treated in the analysis to assess influence of the reward messages. The study design was a 2×2 factorial design (state and reward) with three levels of nesting (state, estuary, and site) (Table 1). Owing to differences in growth rates, insufficient numbers of legal-size fish were available to stock all estuaries during the same month. Thus one estuary in each state was stocked in the fall of 1996 and the remaining estuaries were stocked the following spring and summer. However, each stocking group was available for capture during the fall season when fishing pressure is heaviest (Wenner[3]). Percent return data were arcsine square-root transformed prior to analysis. Return data were analyzed by using a two-way analysis of variance (ANOVA) with significance determined at $P \leq 0.05$. The initial analysis examined all reported or "cumulative" data. The data were then partitioned in two additional ways: by single returns and survey data.

Single returns

This data set was the most restrictive. The assumption was that the partitioned data would be free of any potential bias associated with captures of multiple fish, or with monetary rewards or interactions with project staff.

Survey data

The data were partitioned according to the angler's answers during the interview to determine whether the inducement of a $100 dollar reward changed his or her reporting behavior. This data set included all tags reported individually, all tags of the same message reported as multiples, and all $100 tags. However, it excluded "reward" tags in instances where answers during the interview suggested that the angler's behavior had been changed by capturing a fish with a "$100 reward" tag.

Mean data for each of these analyses were reported with standard errors.

Results

Nearly 95% of tags that were returned were reported within 160 days after release of fish. More fish with "reward" tags were reported than those with "$100 reward" tags in one of the 12 release sites. Overall in SC, 151 anglers reported capture of 203 fish with tags. Anglers reported capture of 1–9 red drum per trip. One hundred

[3] Wenner, C. 1997. Personal commun. South Carolina Department of Natural Resources, 217 Ft. Johnson Rd. Charleston, SC 29422-2559.

and nineteen anglers in SC (79.0% of total anglers) reported only one tagged fish during the study. In GA, 184 anglers reported capture of 226 tagged fish. Single reports in GA represented 80.4% (n=148) of the total catch of tagged fish. The overall return level for all fish reported in SC (22.7 [±1.8]%) was not significantly different from that in GA (25.8 [±4.1]%) (P=0.8129, F=0.07) (Table 2). For the cumulative data, no significant differences were detected between "$100 reward" (27.8 [±3.3]%) and "reward" tags (20.8 [±2.7]%) (P=0.0724, F=12.33) (Table 2). There were also no statistical differences in the cumulative data among the estuaries within states (P=0.0604, F=4.07) (Table 2) and no detectable interaction between state and reward or reward and estuary within states, from the high variability in the cumulative data among estuaries and sites (52.5% and 47.5% of total variation, respectively).

Single returns

To further restrict the potential for bias caused by interaction of different reward messages or caused by the project biologist, capture reports were partitioned to include instances where an angler returned only one tag during the entire study. Overall, no significant differences (P=0.1215, F=6.76) were detected between the single returns of "reward" (11.6 [±1.1]%) and "$100 reward" (15.0 [±2.5]%) treatments within SC. This was also the case in GA (P=0.1215, F=6.760 where 15.1(±2.9)% of "reward" tags were returned, as compared with 17.6 (±2.7)% for "$100 reward" tags (Table 3). In addition, when data were compared between states, no differences were detected (P=0.6152, F=0.35). However, when single returns among estuaries were compared, Wassaw Sound in GA (Fig. 1) yielded significantly higher returns (P=0.0126, F=7.95) than any of the other estuaries where fish were released (Table 3).

Survey data

In SC, 52% of respondents indicated that they had previously caught tagged fish. Of those, several anglers admitted that they had not routinely reported tags. Additionally, others (16%) indicated that they would not have reported the tag if it had not been worth $100. In one extreme case an angler who reported six "$100 reward" tags and an equal number of "reward" tags at once, indicated that he would not have turned in an individual "$100 reward" tag because in his words "he did not need the money."

In GA, 29% of anglers had caught a tagged fish prior to the study; however only 7 (5%) said that they would not turn in tags worth less than $100. In light of this information, the return data were partitioned to eliminate potential bias that would result from encountering a "$100 reward" tag. This partitioned data set revealed that significantly fewer (P=0.0310, F=30.81) unbiased "reward" tags (14.3 [±2.1]%) were returned in SC than "$100 reward" tags (25.5 [±2.3]%) (Table 4). This was also true in GA, where 19.1(±4.3)% of "reward" tags were unbiased returns, as compared with 30.1 (±6.4)% of "$100 reward" tags ($P$=0.0310, F=30.81) (Table 4).

Table 2

Cumulative mean return level (%) and standard error for red drum tagged with one of two reward messages ("reward" or "$100 reward"). No significant differences were detected between reward message, estuary, or state.

	Return level	
Release location	"Reward" (%)	"$100 reward" (%)
Charleston Harbor	23.1 ±0.9	25.8 ±2.2
Calibogue Sound	16.7 ±4.7	25.2 ±4.6
South Carolina (mean)	19.9 ±2.6	25.5 ±2.3
St. Simons Sound	13.9 ±0.6	19.2 ±2.2
Wassaw Sound	29.3 ±8.0	40.9 ±9.0
Georgia (mean)	21.6 ±5.0	30.1 ±6.4
Overall mean	20.8 ±2.7	27.8 ±3.3

Table 3

Mean tag return level (%) and standard error for red drum tagged with one of two reward messages ("reward" or "$100 reward"). There were no significant differences in return levels by reward message within or among estuaries with the exception of those from Wassaw Sound which were significantly higher (P<0.05 noted by *) for both reward messages than any other estuary. SC = South Carolina; GA = Georgia.

	Tag message	
Release location	"Reward" (%)	"$100 reward" (%)
Charleston Harbor, SC	13.3 ±1.6	15.1 ±5.3
Calibogue Sound, SC	9.9 ±1.0	14.8 ±2.0
South Carolina (mean)	11.6 ±1.1	15.0 ±2.9
St. Simons Sound, GA	9.9 ±1.6	13.0 ±1.6
Wassaw Sound, GA	20.2 ±3.8*	22.1 ±3.7*
Georgia (mean)	15.1 ±2.9	17.6 ±2.7
Overall mean	13.3 ±1.6	16.3 ±1.8

Discussion

Overall return levels for the tagged fish released in our study were similar to levels of angler return for red drum in each state's fishery-dependent tagging programs (Wenner[3], Woodward[4]). Because of high variability within estuaries, there were no significant differences between returns of "reward" and "$100 reward" according to the analysis of cumulative return data. The high variability

[4] Woodward, A. G. 1997. Personal commun. Georgia Department of Natural Resources, 1 Conservation Way, Brunswick, GA 31523.

Table 4

Mean return level (%), standard error, and range for unbiased data (adjustments based on verbal interviews) for red drum tagged with one of two reward messages ("reward" or "$100 reward"). Return data for the "$100 reward" message were significantly higher ($P<0.05$) for each estuary, state, and overall than those for the "reward" message.

	Tag message		Unbiased reporting level[1] (%)	
Release location	"Reward" (%)	"$100 reward" (%)	Mean	Range
Charleston Harbor	17.3 ±1.3	25.8 ±3.9	67.1	57–78
Calibogue Sound	11.3 ±6.3	25.2 ±8.0	44.8	19–67
South Carolina (mean)	14.3 ±5.2	25.5 ±5.6	56.7	—
St. Simons Sound	11.7 ±2.1	19.2 ±3.9	60.9	41–82
Wassaw Sound	26.5 ±10.4	40.9 ±15.7	64.8	56–79
Georgia (mean)	19.1 ±10.6	30.1 ±15.6	63.4	—
Overall mean	16.7 ±6.2	27.8 ±11.5	60.1	19–82

[1] Example: Charleston Harbor: "$100 reward" tags reported = 100% · 17.3/25.8 = 67.1% reporting level for "reward" tags.

between sites within the same estuary was unexpected. In addition, variation between estuaries in the same state made comparisons between states difficult. However, "reward" tags were returned less often than "$100 reward" tags from 11 of the release sites in the unpartioned data set. After identifying and excluding possible sources of bias, we found that there were statistically significant differences between reporting level of "reward" and "$100 reward" tags in all areas (Table 4). The range of 19–82% in levels of reporting between sites was more variable than anticipated (Table 4). Removal of the suspected biased anglers from the data set resulted in a mean unbiased reporting level of 67.1% in Charleston Harbor and 44.8% in Calibogue Sound (Table 4). Unbiased reporting in GA was somewhat higher than in SC (63.4% vs. 56.7%). The fact that significant differences were found only after biased angler data were removed from the data set illustrates that a small number of skilled anglers can have an effect on fisheries-dependent data. Their failure to report tags may be due to a lack of novelty in encountering tagged fish, or to insufficient reward incentives (having already received a number of t-shirts, fishing caps, etc.). These data suggest that use of noncash rewards is beneficial only for the first time an angler catches a tagged fish and decreases as anglers catch additional tagged fish. Further repeated exposure to tagging programs within each state eventually results in angler ambivalence and reduced cooperation. This indifference is of particular concern with the use of a constant regional reporting rate as described by Hoenig et al. (1998). A decreasing rate of tag return could be mistaken for lower harvest, reduced fishing effort, poor survival, or increased population size.

Lack of differences in reporting levels between "reward" and "$100 reward" in the single-return (one fish) partition of data (Table 3) confirms that anglers who capture many tagged fish per trip or per season (who were omitted from this data set) significantly influence reporting. Single return-data also suggest that anglers who catch fewer fish (tagged or not tagged) are more likely to report captures of tagged fish regardless of reward amount. Considering the impact a few skilled anglers can have on tag reporting estimates, these results demonstrate the need for further evaluation of the interaction between tagging programs and angler behavior. The 50% reporting level currently used by managers is approximately a 17% underestimate (50/60=0.83) of actual reporting recorded for the red drum fishery in SC and GA. Continuing to use the 50% reporting estimate for this fishery will be more conservative than using the actual reporting level (λ) to calculate angler recovery rate (θ). Reporting was also extremely site specific, and application of data from one site to a broader area may not be appropriate. Ideally tag-recapture models should be weighted by site-specific reporting information to account for this variability which could be accomplished by regular deployment of high value (≥$100) reward tags within each system to gauge angler reporting. Even if offering a $100 does not result in 100% reporting, as Nichols et al. (1991) suggested, it may yield the highest reporting possible with monetary incentives, meaning that our unbiased reporting may have been slightly overestimated. Regardless, this approach is still more accurate than that of adopting a regional average. Our results emphasize that researchers need to conduct controlled tag reward studies regularly and also to offer sufficient rewards in order to avoid under reporting. Furthermore, tag reports must be followed up with angler interviews to determine attitudes and give managers an opportunity to remove bias from the data (Reinecke et al., 1992, Zale and Bain, 1994, Pegg et al., 1996).

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Age, growth, and mortality of the Mayan cichlid (*Cichlasoma urophthalmus*) from the southeastern Everglades

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Abstract—Mayan cichlids (*Cichlasoma urophthalmus*) were collected monthly from March 1996 to October 1997 with hook-and-line gear at Taylor River, Florida, an area within the Crocodile Sanctuary of Everglades National Park, where human activities such as fishing are prohibited. Fish were aged by examining thin-sectioned otoliths, and past size-at-age information was generated by using back-calculation techniques. Marginal increment analysis showed that opaque growth zones were annuli deposited between January and May. The size of age-1 fish was estimated to be 33–66 mm standard length (mean=45.5 mm) and was supported by monthly length-frequency data of young-of-year fish collected with drop traps over a seven-year period. Mayan cichlids up to seven years old were observed. Male cichlids grew slower but achieved a larger size than females. Growth was asymptotic and was modeled by the von Bertalanffy growth equation L_t=263.6(1–exp[–0.166(t–0.001)]) for males (r^2=0.82, n=581) and L_t=215.6 (1–exp[–0.197(t–0.058)]) for females (r^2= 0.77, n=639). Separate estimates of total annual mortality were relatively consistent (0.44–0.60) and indicated moderate mortality at higher age classes, even in the absence of fishing mortality. Our data indicated that Mayan cichlids grow slower and live longer in Florida than previously reported from native Mexican habitats. Because the growth of Mayan cichlids in Florida periodically slowed and thus produced visible annuli, it may be possible to age introduced populations of other subtropical and tropical cichlids in a similar way.

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The Mayan cichlid, *Cichlasoma urophthalmus* (Günther), is native to the fresh and brackish waters of the Atlantic slope of Central America from Mexico to Nicaragua (Miller, 1966), where it is exploited commercially in artesanal fisheries and aquaculture (Martinez-Palacios and Ross, 1992). The first collections of the Mayan cichlid in the United States were made in 1983 from a freshwater habitat and a mangrove creek within Everglades National Park, Florida (Loftus, 1987). Although it remains unknown how or where Mayan cichlids first entered Florida waters, there is evidence that the discovery of this exotic fish was made shortly after their introduction (Loftus, 1987). Since their discovery, Mayan cichlids have expanded their range to include a variety of habitats from Naples (26°05′N, 81°48′W) to West Palm Beach (26°45′N, 80°04′W). The species remains abundant in the man-made freshwater canals and estuarine mangrove habitats of the region (Trexler et al., 2000).

The introduction of the Mayan cichlid into southern Florida has had both economic and ecological significance. This species supports a small sport fishery because it is edible, attractive, and aggressively takes baits and artificial lures (Shafland, 1996). Anglers, however, have mixed feelings towards this fish because it readily takes artificial baits and fights hard on light tackle, and it can interfere with the pursuit of larger gamefishes, such as the common snook (*Centropomus undecimalis*). In some areas, the Mayan cichlid is the most common fish caught by recreational anglers and is targeted by subsistence anglers. There is concern, however that the interaction between Mayan cichlids and native fishes could alter the ecology of the Everglades and Florida Bay region. Although the role of Mayan cichlids as food for higher trophic-level fishes has not been quantified, they themselves are omnivorous and prey upon native fishes (Martinez-Palacios and Ross, 1988; Howard et al.[1]).

Previous studies of the Mayan cichlid have focused almost entirely on its suitability for aquaculture in Mexico (e.g.

[1] Howard, K. S., W. F. Loftus, and J. C. Trexler. 1995. Seasonal dynamics of fishes in artificial culvert pools in the C-111 basin, Dade County, Florida. Final Rep. CA5280-2-9024, 34 p. and append. South Florida Research Center, Everglades National Park, Homestead, FL.

Martinez-Palacios and Ross, 1986; Flores-Nava et al., 1989; Ross and Beveridge, 1995) and on the potential for range expansion in the United States (e.g. Stauffer and Boltz, 1994). Few studies have addressed the life history of the Mayan cichlid, and only scant information exists on the age structure and growth rate of this species. From the seasonal length-frequency distributions for Celestun Lagoon, Mexico, Martinez-Palacios and Ross (1992) concluded that Mayan cichlids from 70 to 130 mm standard length had completed their first spring and were reproductively active, whereas individuals from 131 to 200 mm standard length had entered their second reproductive year. Observing no fish >200 mm, Martinez-Palacios and Ross (1992) concluded that the population of Mayan cichlids in the lagoon comprised fast-growing fish with one, or two (rarely), reproductive seasons in their lifetimes. Aging of Mayan cichlids using a validated method is needed to determine the accuracy of previously reported age and growth estimates and to compare the age structure between populations from Mexico and Florida. Here we provide a first account of the age, growth, and mortality of the Mayan cichlid from Florida waters.

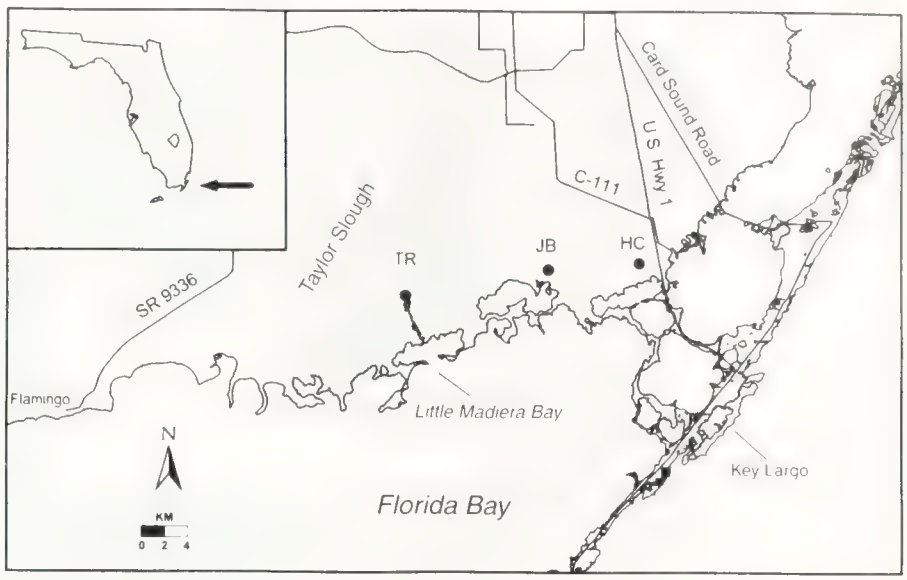

Figure 1

Map of southeastern Florida showing sampling locations (TR=Taylor River, JB=Joe Bay, HC=Highway Creek)

Methods

Mayan cichlids were collected from the dwarf mangrove forests of southeastern Florida. This habitat is dominated by small (0.5–2.0 m tall) red mangrove trees (*Rhizophora mangle*) in an expansive, seasonally inundated wetland of typically shallow water (average maximum depth=30 cm). These mangroves increase in canopy width and height nearer to continuously inundated deeper creeks. The system is inundated mostly by fresh water during July–February but becomes more saline (10–35‰) during the dry season (March–June).

Cichlids <65 mm standard length (SL) were collected by using drop traps (Lorenz et al., 1997) to determine when Mayan cichlids first recruit. Drop-trap samples were collected every six weeks from August 1990 to September 1996 at Highway Creek, Joe Bay, and Taylor River (Fig. 1). Larger cichlids (>65 mm SL) were collected by using hook-and-line gear comparable to that used in other studies (Martinez-Palacios and Ross, 1992). Hook-and-line collections were conducted monthly from March 1996 to October 1997 in Taylor River, a major freshwater distributary of the Everglades emptying into northeastern Florida Bay. Each fishing effort continued until approximately 40 fish were obtained. Fish collected by both methods were measured (SL and total length [TL], mm), weighed to the nearest 0.1 gram, and their sex was determined macroscopically when possible (Faunce and Lorenz, 2000). Fish captured during 1994–97 were used for age-and-growth analyses. All lengths reported hereafter are standard lengths.

Sagittal otoliths were removed, blotted dry, and stored in vials until they were sectioned. The left sagitta, unless broken, was used for age determination. Otoliths were sectioned by using a low-speed Beuhler Isomet saw with diamond blade. Three or four 0.5-mm thick transverse sections, one through the core, were cut and mounted on microscope slides with Histomount™ adhesive and allowed to dry. Sagittae from fish <100 mm were embedded in Spurr, a high-density plastic medium (Secor et al., 1992) and a 1–2 mm thick transverse section containing the otolith core was then cut. The sections were mounted on a microscope slide with Crystal Bond™ 509 adhesive, and polished with wet and dry sandpaper of grit sizes 220–2000 until growth rings were visible. A polishing cloth with 0.05-gamma alumina powder was used to remove scratches.

A standardized protocol for interpreting otolith growth zones was followed. When viewed with reflected light, the transverse sections of Mayan cichlid otoliths had two distinct regions: 1) an "inner region" extending from the core to the first visible opaque zone (ring), and 2) an "outer region" extending from the first visible opaque zone to the edge of the otolith (Fig. 2). The inner region was typically more opaque than the outer region and sometimes contained a visible growth zone or numerous check marks, or both. Unfortunately, these marks were difficult to interpret, inconsistent between sections from individual fish, and in many cases absent altogether. Consequently, we did not count any marks from the inner region in our age estimations. However, the translucent appearance of the outer region of the otolith made it possible to count distinct, separate, opaque rings when present. The number of rings

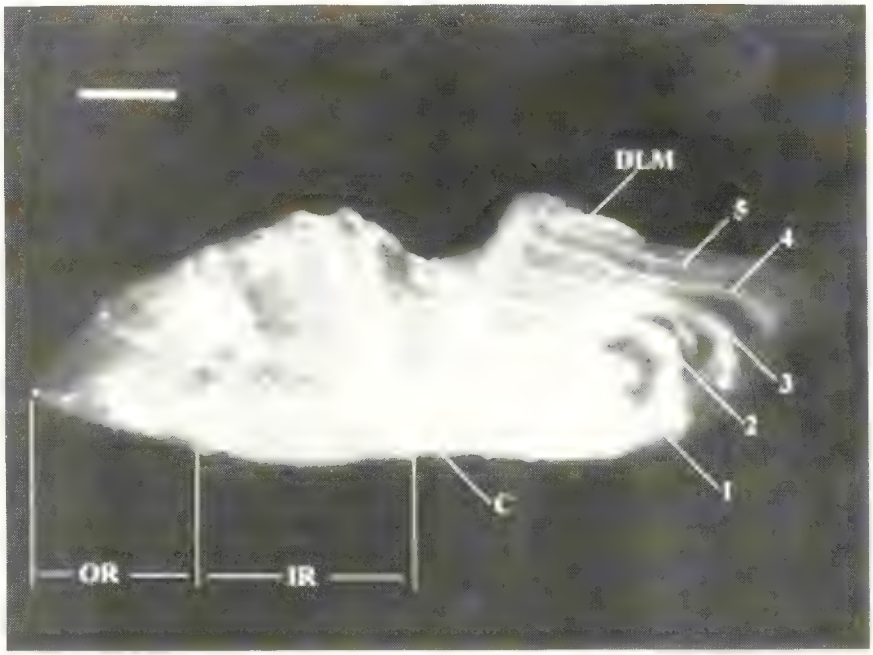

Figure 2

Transverse section of a six-year-old Mayan cichlid (*Cichlasoma urophthalmus*) otolith showing the outer region (OR), inner region (IR), and five visible annuli (1–5). Note that the first annulus (1) corresponds to the fish's second year of growth. A ring corresponding to the first year of growth was not consistently visible and was therefore not counted. Measurements for marginal-increment analysis were made on an axis adjacent to the sulcal ridge from the core (C) to the dorsolateral margin (DLM). Scale bar=500 μm.

on each otolith section was counted independently by two readers using compound microscopes, and the results were compared. If there was a discrepancy in the counts between readers, the section was re-examined. If a consensus could not be reached between the readers after the third reading, the otolith was excluded from the study.

Linear regression was used to determine the relationship of otolith radius to standard length and marginal-increment analysis was used to determine the periodicity of ring formation. Distance from the core to the proximal edge of each ring and to the dorsolateral margin of the otolith (otolith radius) was measured (Fig. 2). Measurements were made with a digital-image processing system along an axis adjacent to the sulcal ridge. The distance from the outermost ring to the dorso-lateral margin (i.e. marginal increment=MI) was plotted by month (marginal increment analysis). Because the majority of Mayan cichlids in Taylor River spawn during May and June (Faunce and Lorenz, 2000), and ring formation occurred during January–May, we assigned each fish a biologically realistic median hatching date of 1 June. Fish collected prior to 1 June that had not yet formed a new opaque ring (=high MI), and all fish collected after 1 June, were assigned a yearly age equal to their ring count. Fish collected before 1 June that had already formed a new opaque ring (i.e. an "early" ring) were assigned a yearly age of one less than their ring count. To compare the timing of ring formation between age groups, marginal-increment analysis was performed on pooled ages 0–3 and 4–7 because our monthly sample sizes for individual age classes were insufficient for this analysis.

We used linear regression to determine the relationship between standard length and total length for all hook-and-line caught fish. The relationship between standard length and total weight was calculated separately for each sex with $\log_{10}$-transformed data. Analysis of covariance (ANCOVA) was used to test for significant differences between the slopes and intercepts of male and female length-weight relationships. Length-frequency distributions for males and females caught with hook-and-line were compared by using the Mann-Whitney rank sum t-test. Non-linear least squares procedures (SAS, 1989) were performed on final observed age-at-length data to estimate parameters for the von Bertalanffy growth equation

$$L_t = L_\infty (1 - \exp[-K(t - t_0)]),$$

where L_t = the standard length (mm);
L_∞ = the asymptotic length;
K = the Brody growth coefficient;
t = the age (years); and
t_0 = the age at zero length (von Bertalanffy, 1957).

To increase the number of observations used for fitting the growth model, we back-calculated past size-at-age information for each sexed fish using the Fraser-Lee method following Devries and Frie (1996);

$$L_i = [(L_c - a)/S_c]S_i + a,$$

where L_i = the back-calculated length of fish when the i^{th} increment was formed;
L_c = the length of fish at capture;
S_c = the otolith radius at capture; and
S_i = the otolith radius at the i^{th} increment.

The slope, $(L_c-a)/S_c$, was calculated for each fish as the slope of a line connecting two points: (S_c, L_c) and $(0, a)$. The y-intercept parameter a was determined from the relationship between otolith radius and standard length for all fish, and should approximate the fish length at which otolith radius equals zero (Devries and Frie, 1996). Because we could not accurately determine the sex of each fish <70 mm, fish whose sex could not be determined were included in the fitting of both male and female growth curves.

Catch curves were analyzed with two methods to determine annual mortality rates for Mayan cichlids. Survival rate (S) and its respective variance were estimated by using the empirical abundance data (Robson and Chapman, 1961) and the regression of the natural logarithm of year-class abundance (Ricker, 1975). The instantaneous rate of mortality (Z) was derived from the relationship $Z=-\ln(e^S)$. Total annual mortality (A) was computed as $A = 1-S$. The age at full recruitment to the hook-and-line gear based on our catch curve was determined to be four years.

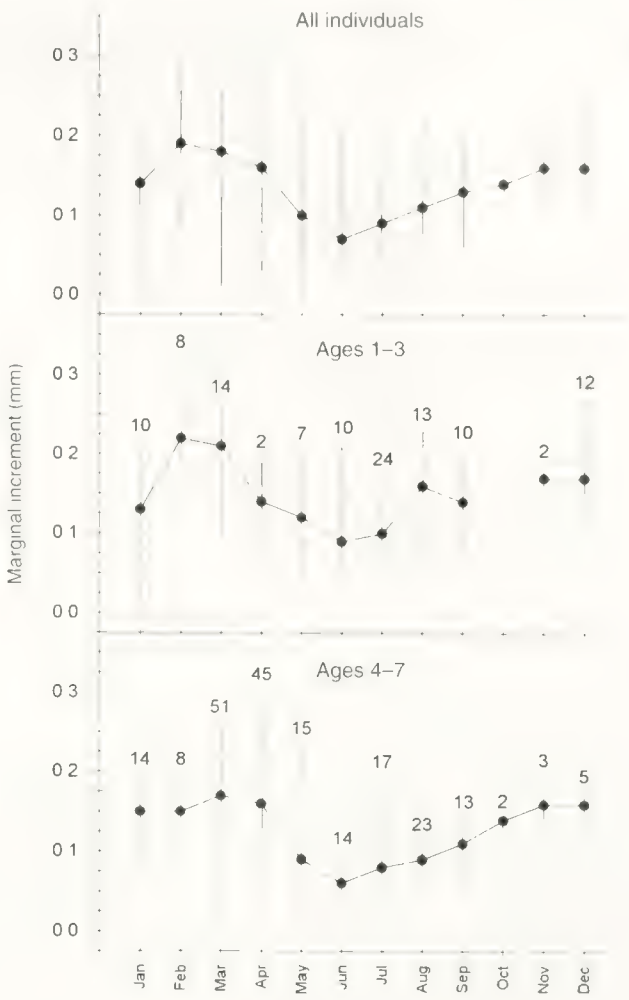

Figure 3

Monthly mean marginal increment and range for all Mayan cichlids and pooled age classes 1–3 and 4–7. Note the consistent annual minimum in June. Numbers indicate sample size.

Results

The fragile nature of Mayan cichlid otoliths caused a high proportion (54%) to be lost during the cutting process. However, only five of the 391 successfully sectioned otoliths were discarded because a consensus between readers could not be reached. A newly formed opaque ring was generally observed in fish captured January–May, and the mean monthly marginal increment reached a single yearly minimum in June for all age classes examined (Fig. 3). These data indicate that the opaque rings observed were annuli.

The growth of young-of-year Mayan cichlids collected with drop traps could be followed by the progression of modal length from monthly length frequencies. Newly recruited fish were present in August (mode=10 mm) and grew to a size of 50 mm by June (Fig. 4). An early spawning event in 1993 (senior author, unpubl. data) produced a smaller-size (20 mm) cohort that was observed in June. Fish with one annulus were much larger (50–149 mm, mean=97 mm) than the size of age-1 fish suggested from our drop-trap data (June mode=50 mm). This information, combined with the presence of marks in the inner region of the otolith, led us to conclude that the first annulus in our age estimations was laid down between January and May of the fish's second year of growth, and we added a year to each individual's total age.

Length-length and length-weight relationships are given in Table 1. As required by the Fraser-Lee method for back-calculation of size-at-age information, otolith radius and standard length were closely related (SL=131.2×OR+4.0247, n=371, r^2=0.80). Analysis of covariance did not detect differences between the slopes of length-weight relationships for males and females ($F_{1,839}$=0.15, P=0.696) but did reveal significant differences between the respective intercepts for males and females ($F_{1,839}$=4.10, P=0.043).

The length of Mayan cichlids at a given age was modeled by the von Bertalanffy growth equation (Fig. 5). Predicted lengths fitted well with the final adjusted observed

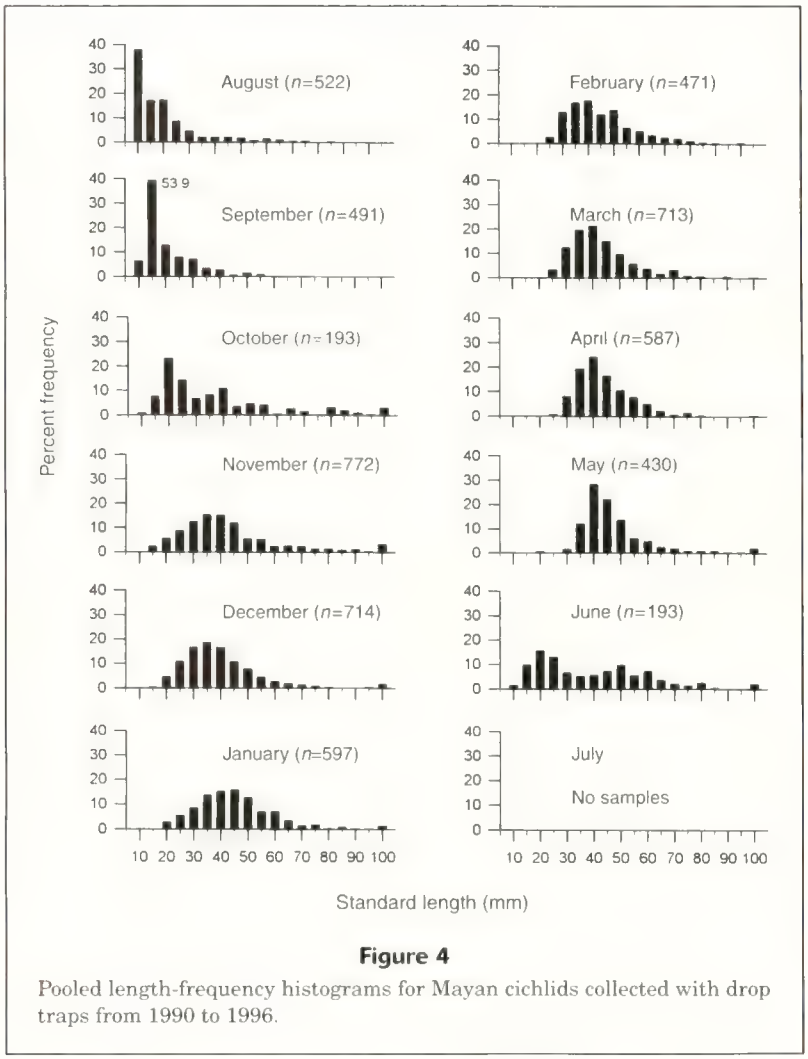

Figure 4

Pooled length-frequency histograms for Mayan cichlids collected with drop traps from 1990 to 1996.

and back-calculated length-at-age data for males (r^2=0.82, n=581) and females (r^2=0.77, n=639). Our observed and back-calculated size of age-1 fish (mean ±1 standard error=45.5 ±10.11 mm, range=33-68 mm, n=22) corresponded well with the modal length of age-1 fish collected in drop-trap samples (50 mm). Differences in the parameter estimates for the von Bertalanffy growth equation were observed for each sex. Males were larger than females for all ages (Table 2). Although males exhibited a slower growth rate (K) and larger maximum attainable size (L_∞) than females, the von Bertalanffy growth model parameters were not significantly different between sexes (95% CI, Table 3). Male and female Mayan cichlids up to seven years old were observed.

The size of fish examined ranged from 21 to 210 mm (median=127 mm, interquartile range=98 mm, n=1046). Males ranged from 69 to 210 mm (median=137 mm, interquartile range=119 mm, n=400), and females ranged from 58 to 190 mm (median=132 mm, interquartile range=115 mm, n=449) (Fig. 6). The length-frequency distribution for males was significantly larger than that for females (P<0.001). The overall ratio of males to females was 1:1.1.

Age-frequency distributions of Mayan cichlids collected by hook-and-line gear suggest that these fish are fully recruited to the fishery at age four (Fig. 7). The majority of males (85.1%) and females (81.5%) were 3–5 years old, and there was a significant difference (Mann-Whitney rank sum t-test, P<0.001) in the age-frequency distribution of males (median=3.67 years, interquartile range=2.12) and females (median=4.78 years, interquartile range=3.86). Total instantaneous mortality (Z), annual survival (S), and annual mortality (A), based on the regression of our catch-curve data, were estimated at 0.57, 0.56, and 0.44, respectively (r^2=0.91, n=3). Robson and Chapman (1961) estimates were Z=0.91, S=0.40 (±0.035), and A=0.60.

Discussion

Transverse otolith sections can be used to precisely age Mayan cichlids from Florida waters. There was a high congruence (98.7%) between the age estimations of each reader. Annuli corresponding to years 2–7 were clearly

Table 1

Length-length, length-weight, and otolith-radius-standard-length regressions for the Mayan cichlid, *Cichlasoma urophthalmus*, from Taylor Slough, Florida. Regressions are in the form $Y = a + bX$. *TL* = total length (mm); *SL* = standard length (mm); *WT* = total weight (g); *OR* = otolith radius (mm); range = sample standard length range in regressions. Values in parentheses are standard errors.

Y	a	b	X	n	Range (mm)	r^2
Sexes combined						
TL	0.6220	1.3067	*SL*	961	40–210	0.997
	(0.2875)	(0.0022)				
SL	–0.1281	0.7631	*TL*	961	40–210	0.997
	(0.2202)	(0.0013)				
SL	4.0247	131.2092	*OR*	371	33–210	0.800
	(3.2740)	(3.4214)				
$\log_{10}WT$	–4.2490	2.9314	$\log_{10}SL$	847	58–210	0.986
	(0.0257)	(0.0122)				
Males						
$\log_{10}WT$	–9.7958	2.9329	$\log_{10}SL$	395	84–210	0.986
	(0.0874)	(0.0178)				
Females						
$\log_{10}WT$	–9.7387	2.9232	$\log_{10}SL$	444	89–182	0.984
	(0.0856)	(0.0176)				

visible on the otoliths. The annulus corresponding to the first year's growth was not consistently clear to the readers, which has been observed in thin-sectioned otoliths of other fish species in Florida. Murphy and Taylor (1994) found that the first annulus was visible only in certain individuals of spotted seatrout, *Cynoscion nebulosus*. Similarly, Murphy and Taylor (1990) found that the annulus corresponding to the first winter or spring was absent in red drum, *Sciaenops ocellatus*. Direct validation of marked otoliths is needed to confirm the presence and location of the first annulus on the otolith of Mayan cichlids.

We observed differences in the growth patterns of males and females that are likely linked to reproduction. Males were larger than females and did not appreciably slow their growth with age. The nearly linear growth of males resulted in a theoretical maximum size (L_∞) of 263.6 mm, well above the ~200 mm commonly observed for this species (Loftus, 1987; Martinez-Palacios and Ross, 1992; present study). Larger males are common in riverine and lagoonal populations of tilapias (Cichlidae) and may have a selective advantage during the reproductive season if they can defend a spawning pit or brood against potential predators (Lowe-McConnell, 1982). Because sperm production requires less energy than egg production (Jalabert and Zohar, 1982), the slowed growth observed in females compared with that for males is likely due to differences in energy budgets during the reproductive season.

No significant differences were found by ANCOVA in the slopes of sex-specific length-weight relationships, but there were significant differences in the intercepts of those lines. Because the actual difference between the *y*-intercepts (weight) of each length-weight relationship was <0.001g, we attribute no biological meaning to the statistical difference and consider the length-weight relationships for both sexes to be equal.

Table 2

Average predicted and observed standard lengths (mm) for male and female Mayan cichlids.

Age (yr)	Predicted	Average observed	Standard error	n
Males				
1	40.3	45.5	2.2	22
2	74.4	74.3	1.12	148
3	103.4	102.0	1.24	152
4	127.9	127.1	1.36	139
5	148.7	147.8	1.66	88
6	166.3	173.0	2.56	28
7	181.1	206	1.32	4
Females				
1	36.4	45.5	2.16	22
2	68.4	70.6	1.05	156
3	94.7	96.8	1.31	160
4	116.3	119.8	1.4	151
5	134.0	137.0	1.59	102
6	148.6	148.1	1.94	45
7	160.6	151.0	3.22	3

Mayan cichlids in Florida were much smaller at a given age than those reported by Martinez-Palacios and Ross (1992) in Mexico. One-year-olds were 33–66 mm in Florida vs. 70–130 mm in Mexico, and age-2 fish were 44–130 mm

Table 3

Parameter estimates for the von Bertalanffy growth model (1957) for Mayan cichlids and associated standard error (SE) and confidence intervals (CI).

Sex	L_∞ (mm)	K	t_0 (yr)	n	r^2
Males	263.66	0.165	0.001	581	0.82
SE	25.15	0.027	0.124		
95% CI	49.28	0.053	0.243		
95% CI range	214.34–312.95	0.112–0.218	0.242–0.244		
Females	215.63	0.197	–0.058	639	0.77
SE	17.33	0.031	0.142		
95% CI	33.96	0.061	0.278		
95% CI range	181.67–249.59	0.136–0.258	–0.336–0.220		

in Florida and 131–200 mm in Mexico. We found a maximum age of seven years, whereas two years was suggested by Martinez-Palacios and Ross (1992). We offer three explanations for these observed differences in the length-at-age data. First, exploitation rates may differ between study areas. Fish in our study came from the Crocodile Sanctuary within Everglades National Park and had not been exposed to fishing mortality. Fishing for Mayan cichlids occurs outside of our study area, and heavy exploitation can select for faster-growing fish with a shorter lifespan (Ricker, 1975). Martinez-Palacios and Ross (1992) suggested that their population was overfished. Second, differences in temperature impact fish growth. Colder winter temperatures in Florida were sufficient to form seasonal marks in the otoliths of Mayan cichlids and may have caused slower growth than in Mexican populations. Third, the seasonal length frequencies of Martinez-Palacios and Ross (1992) were insufficient to accurately identify older year classes. Because growth slows with age, the length-frequency of cohorts corresponding to older age classes can overlap significantly, resulting in erroneously lower age estimates. Future efforts to age Mayan cichlids in Mexico should include thin-sectioned otoliths to evaluate the findings of Martinez-Palacios and Ross (1992).

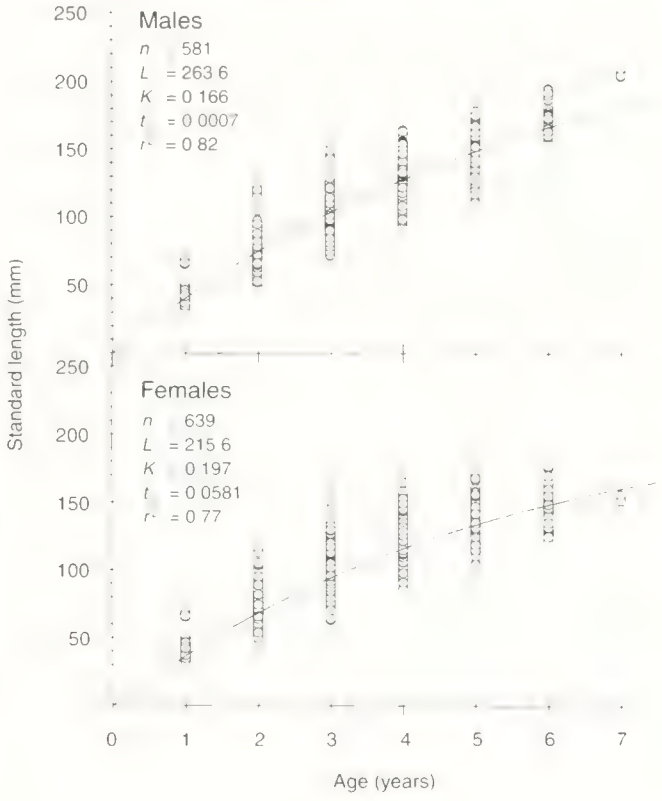

Figure 5

Observed and predicted lengths at age for male and female Mayan cichlids from the von Bertalanffy growth model. n=observed and back-calculated size-at-age information from 148 males and 157 females.

Although the Mayan cichlid has proliferated for over a decade in the natural and man-made habitats surrounding the Everglades, studies are only recently becoming available (e.g. Trexler et al., 2000). More introduced fish species are found in Florida than in any other state in the United States, and 13 of the 18 species with established populations are cichlids (Shafland, 1996). The impact of exotic species on native Florida fishes has been debated: Shafland (1996) proposed no demonstrable effect on native fishes, whereas Courtenay (1997) argued that lack of available data precludes a determination. Trexler et al. (2000) provided empirical data that support Shafland (1996), concluding that although exotics have been credited with native species extinctions in other ecosystems, native Florida fishes are not specialized or restricted to certain habitats and thus are able to cope with the invasion of exotics. Finding no drastic changes in the native ichthyofauna does not necessarily mean that exotic species do not affect indigenous fishes. Exotic species can introduce

numerous stresses not easily quantified, e.g. nest predation, direct predation, and competition for space (Trexler et al., 2000; senior author, unpubl. data). These stresses may affect the population dynamics of native fishes by altering their growth rate, increasing mortality, or decreasing reproductive success. During 1990–99, the Mayan cichlid population underwent a cyclical "boom and bust" pattern of yearly abundance typical of invasive species (Trexler et al., 2000). Why these patterns occur requires a better understanding of the parameters of reproduction, growth, and mortality that drive the population dynamics of this species. The presence of the Mayan cichlid in the Everglades and Florida Bay estuary warrants further research and monitoring efforts in the region to firmly understand the life history of exotics, native fishes, and their role in the ecosystem.

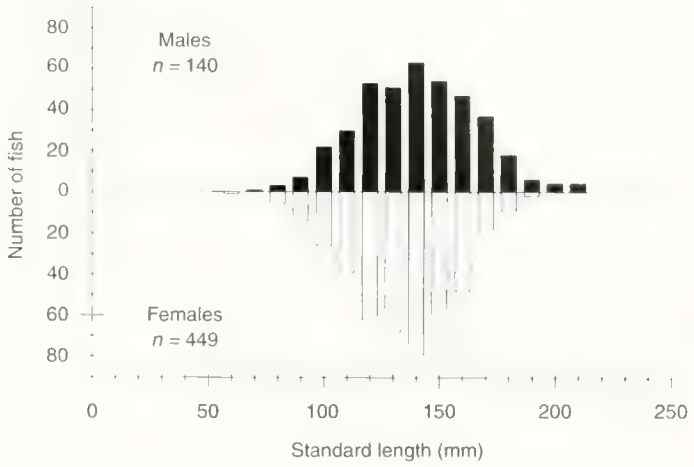

Figure 6

Length-frequency histograms for male and female Mayan cichlids collected with hook-and-line gear.

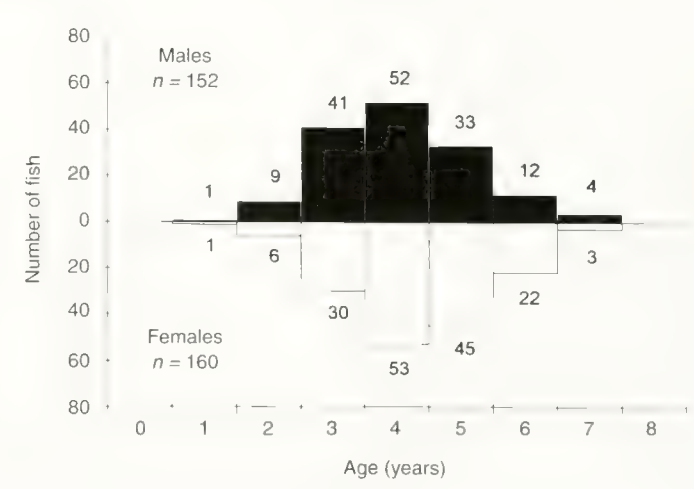

Figure 7

Age-frequency distributions for male and female Mayan cichlids collected with hook-and-line gear. Numbers indicate sample size.

Acknowledgments

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Abstract–We examined seasonal and annual variation in numbers of Steller (northern) sea lions (*Eumetopias jubatus*) at the South Farallon Islands from counts conducted weekly from 1974 to 1996. Numbers of adult and subadult males peaked during the breeding season (May–July), whereas numbers of adult females and immature individuals peaked during the breeding season and from late fall through early winter (September–December). The seasonal pattern varied significantly among years for all sexes and age classes. From 1977 to 1996, numbers present during the breeding season decreased by 5.9% per year for adult females and increased by 1.9% per year for subadult males. No trend in numbers of adult males was detected. Numbers of immature individuals also declined by 4.5% per year during the breeding season but increased by 5.0% per year from late fall through early winter. Maximum number of pups counted declined significantly through time, although few pups were produced at the South Farallon Islands. The ratio of adult females to adult males averaged 5.2:1 and declined significantly with each year, whereas no trend in the ratio of pups to adult females was discernible. Further studies are needed to determine if reduced numbers of adult females in recent years have resulted from reduced survival of juvenile or adult females or from changes in the geographic distribution of females.

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Fish. Bull. 100(1):51–62 (2002).

Population status, seasonal variation in abundance, and long-term population trends of Steller sea lions (*Eumetopias jubatus*) at the South Farallon Islands, California*

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Steller sea lions (*Eumetopias jubatus*) range from southern California along the West Coast of North America through the Aleutian and Pribilof Islands to the Kuril Islands and Okhotsk Sea, Japan (Kenyon and Rice, 1961). Major haulouts and rookeries have historically been centered at the Aleutian Islands and at islands and mainland sites around the Gulf of Alaska, where over 70% of the world population was located in the 1950s and 1960s (Loughlin et al., 1984). In 1990, the species was listed as threatened throughout its range under the Endangered Species Act owing to declines of over 50% from an estimated world population of 240,000–300,000 in the early 1960s to 116,000 individuals in 1989 (Loughlin et al., 1992). Numerically the decline was most severe in the western Gulf of Alaska where 50–80% declines occurred (Loughlin et al., 1992). Reduced juvenile survival appears to be the proximate cause for the decline (York, 1994); ultimate causes, however, are unknown. Effects of long-term environmental change and pollutants on Steller sea lions, and interactions or competition of these sea lions with commercial fisheries are potential contributing causes of this decline (NMML[1]).

In contrast to rookeries in the western Gulf of Alaska, southeast Alaska rookeries have increased by more than 60% over the past three decades (Loughlin et al., 1992). Based on differences in population trends and genetics (Bickham et al., 1996), a distinction has been made between two separate stocks: 1) the eastern stock, ranging from southeast Alaska to California, and 2) the western stock, ranging from the Gulf of Alaska, Aleutian Islands, and Pribilof Islands to Russia (U.S. Federal Register 62:24345–24355). In 1997, the National Marine Fisheries Service listed the western stock as endangered, whereas the eastern stock remained listed as threatened. However, differences in trends between rookeries in southeast Alaska and those in Canada, Oregon, and California may indicate that these areas deserve separate management considerations.

For example, rookeries in Canada and California suffered 40% and 80% declines respectively, from the early 1900s to 1970 (Bigg, 1988; Ainley et al.[2]); declines continued over the past

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[1] NMML (National Marine Mammal Laboratory). 1995. Status review of the United States Steller sea lion (*Eumetopias jubatus*) population. Report of the National Marine Mammal Laboratory, National Marine Fisheries Service, Seattle, WA, 61 p. [Available from National Marine Mammal Laboratory, 7600 Sand Point Way N.E., Seattle, WA 98115-0070.]

[2] Ainley, D. G., H. R. Huber, R. P. Henderson, and T. J. Lewis. 1977. Studies of marine mammals at the Farallon Islands, California, 1970–1975. Final report to the Marine Mammal Commission, Washington D.C. [NTIS publication number PB274046. Available from Point Reyes Bird Observatory, 4990 Stinson Beach, CA 94970.]

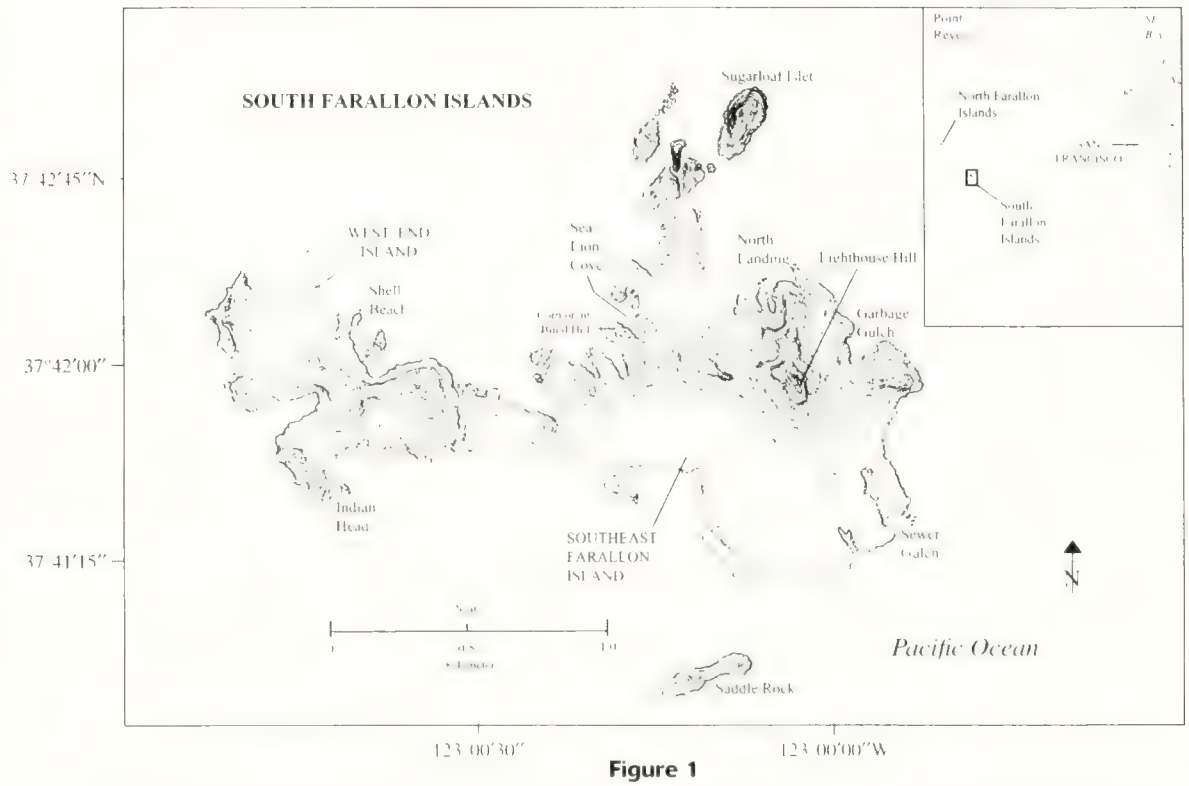

Figure 1

Map of the South Farallon Islands, including Southeast Farallon Island and West End Island. Steller sea lions were counted weekly from 1974 to 1997 from Lighthouse Hill, and several ground areas: North Landing, Cormorant Blind Hill, Sewer Gulch, and Garbage Gulch.

several decades at several California rookeries (Westlake et al., 1997; Sydeman and Allen, 1999; Le Boeuf et al.[3]). Whereas over 2000 Steller sea lions used the Channel Islands in the late 1930s, only 50 animals were observed there in 1959 (Bartholomew and Boolootian, 1960). Pupping at San Miguel Island, an historical rookery, has not been observed since 1981 (NMML[1]). Therefore to better understand patterns and causes of the population decline, trends and status of the eastern stock at southern rookeries deserve further investigation.

The Farallon Islands (37°42′N, 123°00′W), 40 km off the coast of San Francisco, California, are currently one of the most southerly haulout and breeding areas for Steller sea lions; Año Nuevo Island is the only rookery farther south. The Farallon Islands consist of three groups of islands: South Farallones (two islands, Southeast Farallon and West End, separated by a small surge channel), Middle Farallon (an intertidal rock), and North Farallones (four large sea stacks; Fig. 1). Although the status of Steller sea lions in California prior to 1800 was poorly documented, Steller sea lions bred at the Farallon Islands in the 1800s and early 1900s (Allen, 1880; Rowley, 1929) and were the most abundant sea lion in California and at the Farallon Islands from the early to mid 1900s (Rowley, 1929; Bonnot and Ripley, 1948). A large amount of data is now available to examine seasonal variation and long-term trends at the Farallon Islands from historical surveys conducted from 1927 to 1970 by the California Department of Fish and Game (CDFG; Bonnot and Ripley, 1948; Ripley et al., 1962; Carlisle and Aplin, 1971) and from surveys conducted weekly by Point Reyes Bird Observatory (PRBO) from 1971 to 1996. Although maximum numbers declined significantly from 1974 to 1997 for the total population (1.6% per year) and for adult females (3.6% per year; Sydeman and Allen, 1999), it is unknown whether numbers of other age classes also declined and in which seasons declines occurred. To understand proximate causes and consequences of the decline, several questions have yet to be addressed: have reduced pup production and reduced reproductive rates also occurred in recent years?; and what effect has the decline had on the adult sex-ratio? Finally, seasonal variation in counts for different sexes and age classes and variation in the seasonal pattern among years also have not been examined in detail at the Farallon Islands. The objectives of our study were to examine 1) seasonal variation in numbers among sexes and age classes; 2) trends in numbers from 1974 to 1996 by age class, sex, and season; and 3) averages and trends in pup production, reproductive rate, and adult sex-ratio.

[3] Le Boeuf, B. J., K. A. Ono, and J. Reiter. 1991. History of the Steller sea lion population at Año Nuevo Island, 1961–1991. Final report to National Marine Fisheries Service, Southwest Fisheries Science Center, La Jolla, CA. Admin. report LJ9145C, 9 p. [Available from National Marine Fisheries Service, Southwest Fisheries Science Center, P.O. Box 271, La Jolla, CA 92038.]

Methods

Survey methods

PRBO began conducting surveys of pinnipeds at the South Farallon Islands in 1971. In June 1973 surveys were standardized and all Steller sea lions visible on or in the water near the coast of the South Farallon Islands were counted weekly from standard vantage points on Southeast Farallon Island: 1) atop Lighthouse Hill (110 m) with binoculars or a 20–60× spotting scope, 2) from Cormorant Blind Hill (35 m) with binoculars, and 3) from North Landing, Sewer Gulch, and Garbage Gulch with no optical aids (Fig. 1). Most surveys were conducted between 1000 and 1800 hours on Thursdays if visibility was adequate. Beginning in 1977, animals were classified by age class (adult male, subadult male, adult female, immature, yearling, or pup) when possible, primarily by body size. Adult males were distinctive as very large animals with large muscular necks bearing well-developed manes of long, coarse hair on the chest, shoulders, and back. Subadult males were distinguished from adult males by their smaller size and less developed mane. Immature individuals included animals of distinctly smaller size, such as young-of-the-year (after November) and animals likely one to four years of age. The adult female category included animals smaller than subadult males but larger than immature individuals. Pups were distinguishable from June until late November by their thick, dark brown coats, which were later molted and replaced with a lighter brown coat after five to six months of age. Counts were conducted by numerous observers over the years; several observers conducted surveys for over a decade and all observers were trained in identification of sea lions by age class. Counts represent minimum estimates of numbers of sea lions hauled out because only 85% to 90% of the islands were visible from the study's vantage points.

We compared maximum counts taken during the breeding season (June–July) in recent years (1974–97) with counts from surveys conducted a single time during the breeding season (once annually) and intermittently over the years by CDFG from 1927 to 1970. From 1927 to 1938, counts of subadult or adult sea lions (i.e. excluding pups) made by at least two observers from boats were averaged (Bonnot, 1931, 1937; Bonnot et al., 1938). Methods of counting changed after 1938, such that counts after 1938 could only be compared cautiously with earlier years. Surveys were conducted by airplane, blimp, or boat in 1946 and 1947 and by airplane only from 1958 to 1970 (Bonnot and Ripley, 1948; Ripley et al., 1962; Carlisle and Aplin, 1971). Counts from 1946 to 1970 were likely overestimates because observers assumed that all sea lions north of Point Conception were Steller sea lions (many sea lions may have been California sea lions, *Zalophus californianus*) and because pups were likely included in these counts (Bonnot and Ripley, 1948; Ripley et al., 1962). Counts conducted by PRBO since the 1970s targeted only the South Farallon Islands, whereas CDFG counts included the South and North Farallon Islands. Monitoring of the North Farallon Islands since 1970, however, has been sparse. Although the North Farallon Islands are a known haulout area for Steller sea lions, pupping rates are unknown. The North Farallon Islands were surveyed during the breeding season by PRBO in 1977 (when 17 adult females and 1 pup were counted) and in 1983 (when 92 adults but no pups were counted; PRBO, unpubl. data[4]). Because of the exclusion of the North Farallon Islands in recent counts, comparisons with earlier CDFG data were made cautiously.

Under the direction of D. G. Ainley and H. R. Huber, pup production and pup mortality were monitored intensively from 1973 to 1986, when animals were breeding in accessible areas. Breeding areas were checked daily for new pups, and prematurely born and dead pups were noted. Breeding areas shifted from accessible to inaccessible areas over the years. From 1973 to 1975, all full-term pups were born on the more accessible Saddle Rock, a small islet one-quarter mile offshore (Fig. 1), and a few premature pups were born on the mainland. From 1976 to 1983, females pupped in the equally accessible Sea Lion Cove (Fig. 1), perhaps because of reduced disturbance on Southeast Farallon Island, although one pup was observed on Saddle Rock in 1981. Although photographs from the 1930s show large numbers of Steller sea lions on West End (Huber[5]), they were not observed there in recent years until 1983 (one female in the spring). The first pup was born on West End in 1985 (Huber[5]). Currently, the majority of the population is found and all pupping occurs at Indian Head and Shell Beach on West End (Fig. 1); both of these areas are inaccessible and difficult to monitor.

Statistical analyses

Statistical models have been developed that account for effects of observer, and environmental and survey-related covariates on counts of birds and marine mammals (Link and Sauer, 1997, 1998; Calkins et al., 1999; Frost et al., 1999; Forney, 2000). These models can increase accuracy in estimating and power in detecting population trends by reducing variability in counts and correcting biases in trend that result from methodological changes in survey design over time (such as changes in survey dates), particularly when few surveys are conducted during a standard survey window each year (Calkins et al., 1999; Frost et al., 1999). However, environmental covariates could not be included in the statistical models in our study when the full data set was used because observers recorded the times that surveys began and ended on only a few occasions prior to 1983 (41 of 569 surveys, or 7.2% of surveys), such that the majority of data during the first decade of the time series would be excluded. To include the entire

[4] PRBO (Point Reyes Bird Observatory). 1988. Unpubl. data. [Available from W. J. Sydeman, Point Reyes Bird Observatory, 4990 Shoreline Hwy, Stinson Beach, CA 94970.]

[5] Huber, H. R. 1985. Reproduction in northern sea lions on Southeast Farrallon Island, 1973–1985. Final report to the Gulf of the Farallones National Marine Sanctuary, San Francisco, CA, 22 p. [Available from Point Reyes Bird Observatory, 4990 Shoreline Hwy., Stinson Beach, CA 94970.]

time series, standard regression models, including survey date but excluding effects of environmental covariates, were used to examine seasonal patterns and trends. We believe the exclusion of other covariates during statistical modeling had little effect on trend estimates because surveys were conducted consistently over years and over the entire year interval, resulting in large sample sizes (n=1134 surveys conducted; range among years 1974–96: 45 to 52 surveys/year). It is unlikely that population trend estimates were confounded by changes in environmental conditions because no obvious annual trends in environmental conditions over the 22 years of the study (weather and tide data were collected daily [at 1000 hours] at Southeast Farallon Island) were apparent, except for a potential increasing annual trend in sea surface temperature (PRBO, unpubl. data[4]).

Seasonal abundance patterns To examine seasonal abundance patterns, polynomial regression (Kleinbaum et al., 1988) was used to fit a curve to counts pooled over years, 1974 to 1996. Data from 1971 to 1973 were excluded because survey methods were not standardized until the end of 1973. We fitted the regression model by first converting Julian date to orthogonal polynomial variables (linear combinations of the natural polynomial variables that contain the same information as the natural polynomial variables but are uncorrelated to each other) to avoid problems of multicollinearity when using higher-order terms (Kleinbaum et al., 1988). Higher-order terms were then added sequentially until the last term was not significant in the model (forward stepwise procedure, P>0.05). We then added *year* as a variable to the model and tested the *year* × *date* interaction to determine if the seasonal pattern varied significantly among years. To examine seasonal patterns by sex and age class, polynomial regression curves were fitted separately to counts of adult females, males (adults and subadults pooled), and immature individuals as described above. We excluded surveys in which not all individuals were identified by sex and age class (i.e. all surveys before 1977).

Annual abundance trends Because high-order polynomial models were used to address seasonal haulout patterns, annual abundance trends were examined in a separate analysis to simplify results. Seasonal variability in abundance was accounted for in annual trend models by using residuals from the regression of *Julian date* on counts. Assuming exponential rates of change, we log-transformed ($\log_e$) the residuals (centered about the mean count) and regressed the transformed residuals against the variable *year*. Annual rates of change were calculated as $e^{\beta_{Year}} - 1 \times 100\%$, where β_{Year} is the regression coefficient for annual trend (Caughley, 1977). The following groups were analyzed: 1) all animals, by pooling data over all 12 months and sex and age classes; and 2) each sex and age class, by pooling over a) all months, and b) two periods when peaks in counts were observed for some age classes (the breeding [May–July] and late fall through early winter [September–December] seasons). Nonlinearity in trend was assessed by using orthogonal polynomials as described earlier in this article. Assumptions of the regression model were verified by visual inspection of residuals.

Trends in pup production, reproductive rate, and adult sex ratio during the breeding season We used linear regression to test if the decline in maximum pup counts during surveys presented in Sydeman and Allen (1999) was significant. We used only data after 1977, when counts by age class were conducted consistently. Only data from surveys conducted from June to July were included because during the fall, the ability to distinguish young-of-the year from immature individuals was difficult and because an influx of nonnative pups may have occurred. For example, in November 1978, five times the number of pups known to have survived the breeding season and an increased number of adult females were observed (PRBO, unpubl. data[4]). The origin of these young-of-the-year is unknown, but the nearest known pupping areas are Año Nuevo Island and the North Farallon Islands. Although Steller sea lions are present at Point Reyes, no pups have been observed there in the past two decades (Sydeman and Allen, 1999).

To examine averages and trends in adult sex ratio and reproductive rate, we used maximum counts of adult females, adult males, and pups during June and July in each year and linear regression to test for annual trends. Reproductive rate was calculated as the maximum count of pups divided by maximum count of adult females. Because not all pups born were observed during surveys, we increased the maximum count of pups by 57%, the average amount that maximum pup counts underestimated true pup production from 1973 to 1986 (range: 33–90% among years). This average was determined from unpublished data of pup production as determined from daily observations of breeding areas (Huber et al.[6]).

Results

Seasonal abundance patterns

When data from all sexes and age classes were pooled, the seasonal abundance pattern was bimodal; one peak in numbers occurred before and during the breeding season (April–July) and another peak occurred from late fall through early winter (October–December; Fig. 2A). The regression model was complex with significant date and higher-order terms (variables $date^2$ through $date^8$); all P<0.001; adjusted r^2=0.28, n=1134); the variable $date^9$ was not significant (P>0.65). Counts varied significantly with year (P<0.001) and the seasonal pattern varied significantly among years (*date*×*year* through $date^8$×*year*; P<0.001; adjusted r^2=0.61). Total numbers during the peak

[6] Huber, H. R., D. G. Ainley, R. J. Boekelheide, R. P. Henderson, and T. J. Lewis. 1988. Annual and seasonal variation in numbers of pinnipeds on the Farallon Islands, California (Table 3). Final report to the National Marine Mammal Laboratory, National Marine Fisheries Service, Seattle, WA, 35 p. [Available from Point Reyes Bird Observatory, 4990 Shoreline Hwy., Stinson Beach, CA 94970.]

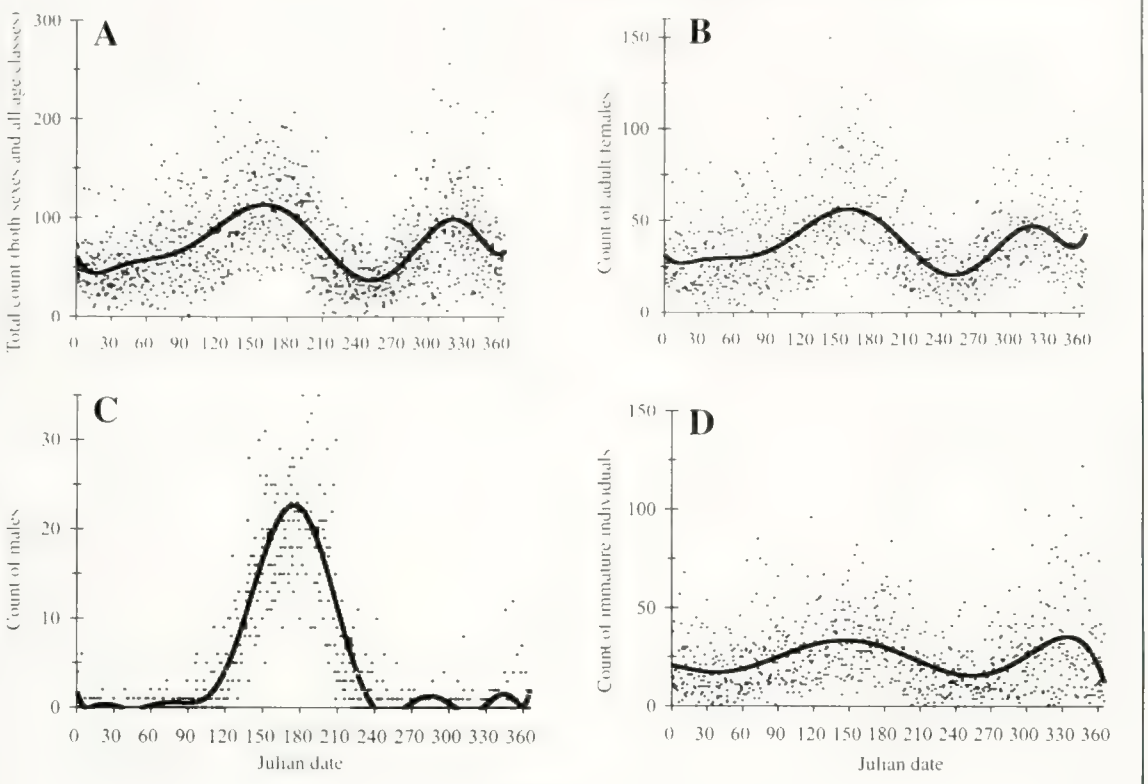

Figure 2

Seasonal variation in counts of Steller sea lions at the South Farallon Islands for (**A**) both sexes and all age classes; (**B**) adult females; (**C**) subadult and adult males; and (**D**) immature individuals and yearlings. Data from 1974 or 1977 to 1996 were pooled. Black dots indicate counts: black lines indicate predicted values from the regression model. Divisions on the *x*-axis approximate months. The best regression model for each group included the variables *date* and $date^2$ through (A) $date^8$ for total counts (adjusted r^2=0.28); (B) $date^8$ for adult females (adjusted r^2=0.22); (C) $date^{12}$ for males (adjusted r^2=0.77); and (D) $date^6$ for immature individuals (adjusted r^2=0.13).

breeding season averaged approximately 100 animals, ranging from 50 to 200 animals; whereas numbers from the late fall through early winter peak were more variable, averaging slightly less than 100 and ranging from less than 10 to 300 animals (Fig. 2A).

Seasonal patterns varied among sexes and age classes (Fig. 2, B–D). Counts of adult and subadult males peaked only during the breeding season (Fig. 2C), whereas counts of adult females and immature sea lions were bimodal (Fig. 2, B and D). When models including the variables *date* through $date^8$ were fitted to data for adult females and immature individuals separately, the seasonal pattern differed significantly between the two groups *(age class, year,* and all interaction terms: all $P<0.001$). Counts of immature sea lions were less peaked during the breeding season than those of adult females and, in contrast to the average adult female pattern, numbers during winter peaked on average slightly higher than during the breeding season (Fig. 2, B and D).

The seasonal pattern varied significantly among years for all age classes (*year* and *year*×*date* interactions for adult females and immature individuals: $P<0.001$, and for subadult and adult males: $P<0.05$). Variation in seasonal pattern among years was complex but several general patterns could be noted. A gradual shift in the peak breeding season count from the beginning of May in 1974 to the beginning to middle of June in 1979 was evident (Hastings and Sydeman[7]). The late fall–winter peak was very pronounced from 1984 to 1986, with maximum counts of 200 to 300 animals (Hastings and Sydeman[7]), most of which were immature individuals. From 1992 to 1996, the seasonal abundance pattern was muted with equal or higher numbers in the winter than in the breeding season (Hastings and Sydeman[7]).

[7] Hastings, K. K., and W. J. Sydeman. 1998. Status, seasonal variation and long-term trends in numbers of Steller sea lions, *Eumetopias jubatus,* at the South Farrallon Islands, California: 1927–1996. Final report to the National Marine Fisheries Service, Southwest Fisheries Science Center, La Jolla, CA, 30 p. [Available from Point Reyes Bird Observatory, 4990 Shoreline Hwy., Stinson Beach, CA 94970.]

Table 1

Linear rates of change in counts of Steller sea lions on the South Farallon Islands by season, sex, and age class. Rate of change per year was calculated by 1) removing the effect of date on counts (i.e. by using residuals from regression of date on counts), and 2) log-transforming ($\log_e$) the sum of the residuals added to the mean count. * indicates significant trends ($P<0.05$) from regressions. n = sample size.

Age class	% change	β_{Year}	SE (β_{Year})	P	n
All animals					
All months	-0.44	-0.0044	0.0027	0.03*	1134
Adult females					
All months	-3.16	-0.0321	0.0032	<0.001*	866
Breeding season (May–Jul)	-5.89	-0.0607	0.0081	<0.001*	217
Late fall through early winter	2.50	0.0247	0.1637	0.80	280
Males (breeding season)					
All males	1.12	0.0111	0.0050	0.03*	217
Bulls	0.16	0.0016	0.0022	0.63	217
Subadult males	1.94	0.0192	0.0086	0.03*	217
Immature sea lions					
All months	0.55	0.0055	0.0019	0.004*	866
Breeding season	-4.51	-0.0461	0.0168	0.007*	217
Late fall through early winter	4.97	0.0485	0.0078	<0.001*	280

Annual abundance trends

Although visual inspection showed that residuals of log-transformed counts were not normally distributed, a square-root transform of counts normalized residuals. We report trend estimates from log-transformed counts because results of statistical tests for trends with log- and square-root-transformed data were identical.

After removing seasonal effects (i.e. residuals from regression of *date* on count were used), all sexes and age classes showed significant trends but in different directions (Table 1). When data from all sexes and age classes were pooled, the trend was complex (variables *year* through *year*^{3}: all $P<0.05$; n=1134; Fig. 3A). Counts were highest in the late 1970s to early 1980s and declined only slightly during the late 1980s to early 1990s. A slight (–0.4% per year) linear decrease in total counts (pooling over months, sexes, and age classes) with *year* was significant ($P<0.05$; Table 1). Adult female counts declined significantly although the rate of decline slowed in recent years (variables *year* and *year*^{2}: $P<0.01$; n=866; Fig. 3B). Counts of adult females declined significantly during the breeding season (variables *year* and *year*^{2}: $P<0.01$; n=217; Fig. 3B), whereas no trend during late fall and early winter was evident (P=0.80; Table 1). Linear rate of decline for adult females was –3.2% per year for all months combined and –5.9% per year during the breeding season (both $P<0.001$; Table 1).

In contrast, numbers of males during the breeding season increased linearly with *year* at a rate of 1.1% per year ($P<0.05$; n=217; Table 1). This increase was due to an increased number of subadult males (1.9% per year; $P<0.05$; Table 1; Fig. 3C), whereas the numbers of adult males were stable ($P>0.60$; Table 1). Counts of immature individuals also increased slightly (0.6% per year; Table 1) but significantly when counts from all months were pooled (variables *year* and *year*^{2}: $P<0.01$; n=866; Fig. 3D). The increase was due to the greater numbers of immature individuals from late fall through early winter in recent years (linear trend=5.0% per year, Table 1; *year* and *year*^{2}: $P<0.01$; n=280; Fig. 4D). However, numbers of immature individuals present during the breeding season declined at a rate of –4.5% per year (Table 1; *year*: $P<0.01$; n=217; Fig. 3D).

Trends in pup production, reproductive rate, and adult sex ratio during the breeding season

Maximum pup count from surveys declined significantly from the mid-1970s to the mid-1980s from 15 to 2–4 pups and has remained low in recent years (*year* and *year*^{2}: $P<0.003$; Fig. 4). After adjusting for pups not seen during surveys, reproductive rates of adult females ranged from 2.0% to 21.2% among years, with an average rate of 10.7% (Fig. 4). Although reproductive rate appeared to decline in the 1980s and recovered to 1970s levels in the 1990s, no trend was discernible (*year* and higher-order terms: $P>0.20$; Fig. 4). The ratio of adult females to adult males during the breeding season ranged among years from 10.3:1 to 1.8:1, with an average of 5.2:1 (Fig. 4). The ratio of adult females to adult males declined significantly and linearly with *year* ($P<0.001$).

Discussion

Although the Farallon Islands are an important haulout area for Steller sea lions in California, numbers of ani-

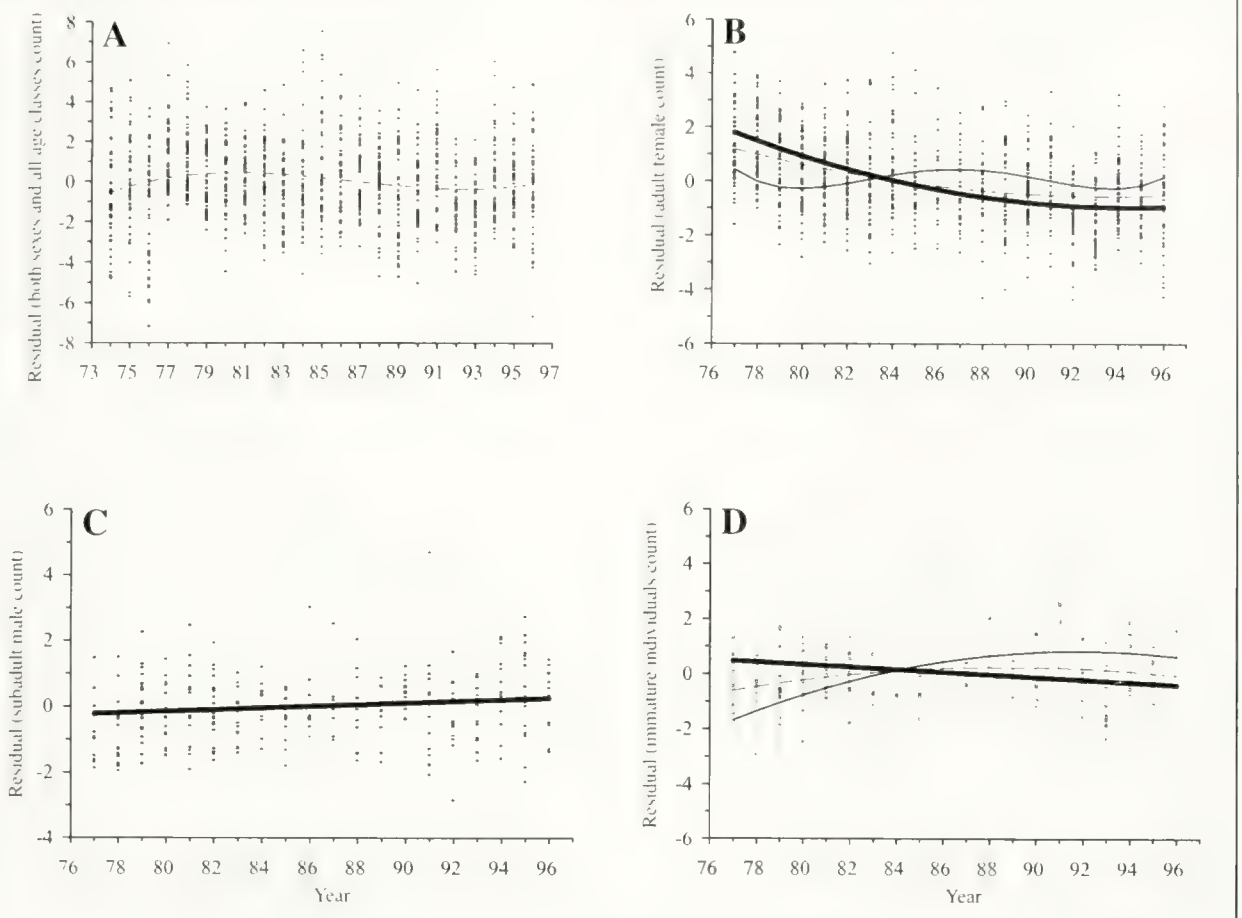

Figure 3

Annual trends in counts of Steller sea lions at the South Farallon Islands from 1974 or 1977 to 1996 for (**A**) both sexes and all age classes; (**B**) adult females; (**C**) subadult males; and (**D**) immature individuals and yearlings. Significant trends in counts, after accounting for survey date (residual centered about the mean count from Figure 2, square-root transformed), are shown for: all months (light dashed line); only counts during the breeding season (May – July; solid black line); and only counts from late fall through early winter (September–December; solid light black line). Results of significance tests using square-root and $\log_e$-transformed counts were identical; Linear rates of change from $\log_e$-transformed counts are shown in Table 1.

mals at the Farallon Islands are currently lower (0.06 of the 1989 statewide count, 0.09 of the count from four major sites) than at the other three major California sites (Año Nuevo Island, St. George Reef, and Sugarloaf Island) which ranged from 0.16 to 0.18 of the 1989 statewide count, and from 0.26 to 0.37 of the count from four major sites (Loughlin et al., 1992). A smaller proportion of the statewide Steller sea lion population has used the Farallon Islands in recent years, compared with population counts in the 1927–30 data, when Farallon animals accounted for 0.11 to 0.14 of the statewide count (Bonnot and Ripley, 1948). Historical pup production at the Farallon Islands is unknown, but both the Farallon Islands and Año Nuevo Island were identified as the two largest and most important Steller sea lion rookeries in the state in the early 1920s (Rowley, 1929). Pup production at the South Farallon Islands over the past two decades has been very low at <30 pups per year and in the last 10 years, at <10 pups per year. Pup production since the mid-1980s, however, may be underestimated owing to the reduced probability of sighting pups since 1984 when pupping areas shifted to West End Island, which is farther away from the survey vantage points. Pup production at other major sites in California included 117–137 pups at Sugarloaf Island and Cape Mendocino in the early 1980s, 115 pups at St. George Reef in 1994, and 230–243 pups at Año Nuevo in 1993–94 (Westlake et al., 1997; NMML[1]).

Reproductive rates of Steller sea lions at the South Farallon Islands were also low; an average of only 0.11 of females present during the breeding season produced pups. This number may be biased low because some immature males may have been included in the adult female count. This ratio is much lower than that for rookeries in British Columbia (>0.70, Pike and Maxwell, 1958), Año Nuevo, California (average of 0.40 to 0.50 from 1962–1990; Le Boeuf et al.[3]) and Ugamak Island, Alaska, where ratio of

pups to females increased from 0.75 to >1.00 from 1968 to 1986 (Merrick et al., 1987). The South Farallon ratio is more typical of peripheral areas of rookeries in Alaska where only 0.01 to 0.09 of females had pups compared with main areas of rookeries where ratios averaged 0.63 to 0.74 (Withrow, 1982).

Similarly, high pup mortality rates observed at the Farallon Islands (average of 0.49 of pups born from February to August, range of 0.33 to 0.90 among years; Huber et al.[6]) are more characteristic of peripheral areas of rookeries where pup mortality ranged from 0.30 to 1.00 compared with 0.10 to 0.12 at main rookery sites (Withrow, 1982). Rookeries had much lower pup mortality rates during the first two months of life than those observed at the Farallon Islands, including Año Nuevo Island, California (0.10, Gentry, 1970), and sites in Alaska (0.03–0.14, Merrick et al., 1987). The frequency of premature pupping (0.40 of those born; Huber et al.[6]) is also very high compared with the frequency at rookeries in Alaska (0.09; Pitcher and Calkins, 1981), Oregon (0.04; Mate, 1973), at Año Nuevo Island (0.02; Gentry, 1970). As at Año Nuevo, most premature pups are born from February to May at the Farallon Islands (0.65 born in April with a range of February to May), whereas full-term pups are born from mid-May to late July (Gentry, 1970; Huber[5]). Causes of the high rate of premature pupping at the Farallon Islands are unknown but may be due to several factors known to cause reproductive failure in pinnipeds, including disease or exposure to pollutants (Gilmartin et al., 1976; Huber[5]), or a prevalence of young, inexperienced, or malnourished females (Pitcher et al., 1998). A high frequency of abortions has been observed at haulout sites rather than at rookeries in Alaska (Pitcher and Calkins, 1981). Low pup production and reproductive rates, coupled with high pup mortality and premature pupping rates, support characterization of the Farallon Islands in recent years as a haulout site or peripheral rookery for this species.

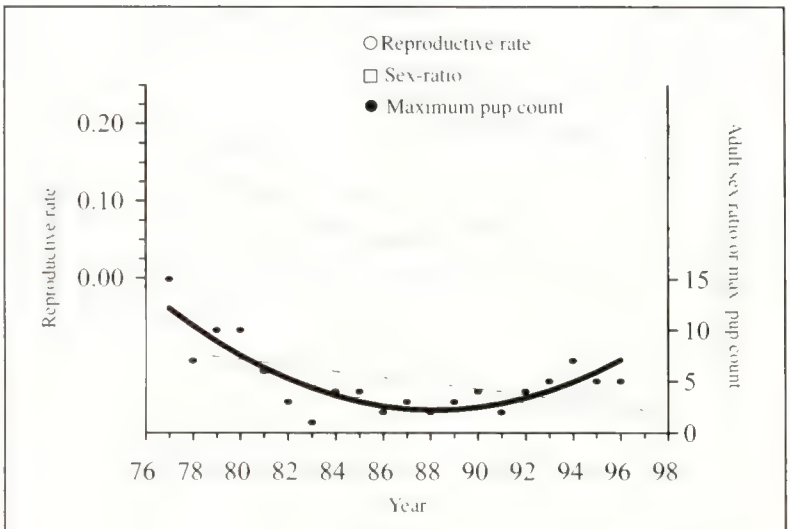

Figure 4

Annual variation in reproductive rate, adult sex ratio, and maximum pup count during the breeding season (June–July) at the South Farallon Islands, 1977–97. Reproductive rate was defined as the maximum pup count divided by the maximum count of adult females per year. Adult sex ratio was calculated as the maximum number of adult females divided by the maximum number of adult males (bulls) counted per year. Significant ($P<0.05$) trends are shown for adult sex ratio (dashed black line) and maximum pup count (bold black line).

Seasonal patterns in counts

Seasonal haulout patterns varied significantly among sexes and age classes. Adult and subadult male attendance was highly seasonal and males were present only during the breeding season. In contrast, adult females and immature individuals were present year-round and their numbers peaked twice (breeding season and from late fall through early winter). Many studies reported the absence of adult and subadult males at California rookeries outside the breeding season, including Año Nuevo Island (Orr and Poulter, 1967) and San Miguel Island (Bartholomew, 1967), and the presence of females and immature individuals at rookeries year-round (Rowley, 1929; Bartholomew, 1967). At Canadian rookeries, males were also generally absent in the winter, but small numbers of females and young of the year usually remained at rookeries throughout the year (Bigg, 1988). Circumstantial evidence suggests males from California migrate northward or males from Southeast Alaska move southward in winter, or both movements take place. Large numbers of males have been seen outside the breeding season off northern California (Fry, 1939), Oregon, Washington (Mate, 1973), and southern Vancouver Island (Bigg, 1988). Total numbers of Steller sea lions are also higher in the winter than in the summer off the Canadian coast (Bigg, 1988); some winter haulouts in Canada consist almost exclusively of males (Bigg, 1988). The earliest evidence for sea lion migrations was provided by the recovery of north-coast native American spearheads from several sea lions killed off southern California in the late 1800s; and in June 1870, a spearhead used by native Alaskans was found in a large male sea lion at Point Arena, California (Scammon, 1874). Seasonal northward movement has also been documented in male California sea lions, which were similarly absent from southern sites outside the breeding season but which ranged up into Washington and British Columbia during winter (Starks, 1921; Fry, 1939; reviewed by Bartholomew, 1967).

In contrast to animals on the Farallon Islands, animals of all age classes and both sexes on Año Nuevo Island were present in significant numbers only during the breeding season from 1967 to 1990 (Le Boeuf and Bonnell, 1980; Le Boeuf et al.[3]). Data from 1962 and 1963 indicated a substantial presence of Steller sea lions at Año Nuevo through the fall and winter (Orr and Poulter, 1965) and therefore the lower numbers and, more recently, near absence of all

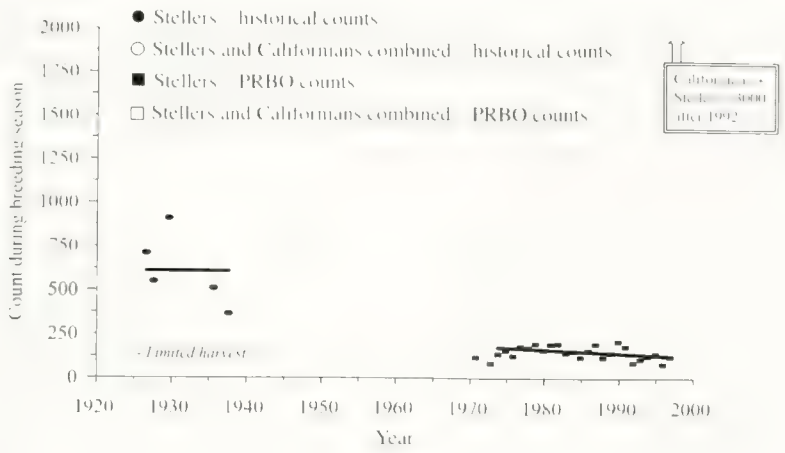

Figure 5

Counts of sea lions at the Farallon Islands during the breeding seasons, from 1927 to 1997. Historical counts, 1927–38: total count from single census per year conducted by boat; includes North and South Farallones and adults and subadults only (Bonnet et al., 1938). Historical counts, 1946–70: total count from a single census conducted each year by airplane, blimp, or boat; includes North and South Farallon Islands and may include pups, subadults and adults. Steller and California sea lions were not distinguished during these surveys. Instead all sea lions north of Point Conception were considered Steller sea lions and those south of Point Conception were considered California sea lions (Bonnot and Ripley, 1948; Ripley et al., 1962; Carlisle and Aplin, 1971). Point Reyes Bird Observatory counts, 1974–97: maximum total counts during June and July from weekly censuses at South Farallon Islands only (North Farallones excluded); includes pups, immature individuals, subadults, and adults. Means or trends over years are shown for Steller counts only (solid black lines) and for counts of Steller and California sea lions combined (dashed lines).

age classes after the breeding season may be a recent phenomenon. Similarly, Steller sea lions of various sexes and age classes were present off Humboldt County, California, only from mid-April to September (Sullivan, 1980).

Diverse seasonal patterns among sites were also evident in Canada and Alaska. In Canada, animals were usually present year-round on rookeries and numbers peaked during July, whereas year-round haulouts showed no marked seasonal variation and a variety of sexes and age classes were present in winter (Bigg, 1988). Winter haulouts were occupied only in the winter and consisted of either only males or a variety of sexes and age classes (Bigg, 1988). In Alaska, many rookeries were abandoned and some haulouts were occupied only in winter; other haulouts and rookeries were occupied year-round (Kenyon and Rice, 1961; NMML[1]). Major seasonal shifts in distribution were not evident in Alaska, although winter counts were substantially lower than summer counts and there was a greater proportion of animals at haulouts than at rookeries in winter (NMML[1]). The diversity in seasonal patterns observed among sites (including rookeries and haulouts) in California and elsewhere has confounded generalizations concerning seasonal haulout patterns, although a general shift from rookeries to haulouts in winter seems to occur throughout most of the species range.

Population status of Steller sea lions in southern and central California

Decline from historical numbers Substantial declines in Steller sea lions at the Farallon Islands have been evident since the 1920s and in recent decades. Numbers declined approximately 75–80% from an average of 600–790 animals from 1927 to 1947 to an average of 150 animals (maximum count) from 1974 to 1997 (Fig. 5). This decline may be overestimated because animals on the North Farallon Islands have not been included in surveys since 1970 and because more animals are likely visible by boat or air than from island-based vantage points (Westlake et al., 1997). However, 85% to 90% of the island is visible from vantage points and therefore effects of incomplete coverage should be small. Although the decline in numbers was severe between 1938 and 1974, the rate of decline cannot be determined for this period because surveys from this period did not distinguish Steller from California sea lions (Fig. 5). These surveys assumed that all sea lions north of Point Conception were Steller sea lions and that all sea lions south of Point Conception were California sea lions (Carlisle and Aplin, 1971). Assessing the status of Steller sea lions from the 1946–70 CDFG counts has been confounded by growth in the California sea lion population

over the same period. For example, California sea lions made up only 20% of the total sea lion count at the Farallon Islands in 1938 (Bonnot and Ripley, 1948); but by the mid 1970s, California sea lions were twice as numerous as Steller sea lions during June and July (Fig. 5).

The role of commercial harvest and direct take or harassment of sea lions by humans in this decline is uncertain. Large numbers of sea lions were hunted in California in the late 1800s for oil, hides, and "trimmings" (which included the whiskers, genitalia, and gall bladder of adult males) that were sold to Chinese markets (Scammon, 1874). Hunting sea lions for oil became unprofitable around 1900 because of the reduction in sea lion numbers and the wide-spread availability of petroleum products (Rowley, 1929). A reduced sea lion harvest for hides, trimmings, and (in Mexican waters) pet food, continued until the end of the 1930s when Chinese markets disappeared with the onset of the Japanese-Chinese war and protests were successful in stopping Mexican harvests (Bonnot, 1951). During the same period, although fewer sea lions were taken by sportsman, fisherman, and collectors for museums and zoos, rookery abandonments and population declines still persisted in Oregon and southern California (Rowley, 1929; Bonnot, 1931). An additional cause for these population declines may have been the sea lion hunts that were introduced by commercial fisheries around 1900 to reduce competition for fish (Bonnot, 1937). For example, a bounty was offered for Steller sea lions in the early 1900s in areas north of California (Rowley, 1929; Bonnot, 1931; Bonnot, 1951).

Although numbers harvested in California are not well documented and the role of harvest in the decline is not obvious, several arguments can be made that declines in Steller sea lions from the 1940s to 1970s were likely not due to effects of harvest alone. During the period of commercial harvest, Steller numbers appeared stable (Bonnot and Ripley, 1948), whereas the 75–80% decline was evident after 1947, after commercial hunting and collections had ended, although harassment by fisherman continued. After 1947, the California sea lion population increased exponentially throughout the state from 3050 in 1947 to a minimum of 18,047 in 1970 (Bonnot and Ripley, 1948; Carlisle and Aplin, 1971), whereas numbers of Steller sea lions on the Channel Islands and at the Farallon Islands declined from 80% to 100% during this period. Large increases in California sea lions were evident after commercial harvesting ended, even though many more California than Steller sea lions were likely hunted commercially, poached, or captured because of difficulty hunting in the steep, rocky intertidal areas frequented by Steller sea lions (Rowley, 1929; Bonnot, 1951). This reasoning suggests that factors in addition to harvest have influenced the population decline. Proposed causes include reduction of the prey base due to overexploitation by commercial fisheries (Ainley and Lewis, 1974), shifts in prey composition due to ocean warming, and competition for food with growing numbers of California sea lions (Bartholomew, 1967).

Human disturbance, however, likely played some role in the decline, in respect of which Steller sea lions may be more affected by human disturbance than California sea lions. For example, the large Steller sea lion rookeries at San Miguel Island and at Seal Rocks, just off San Francisco, were abandoned permanently because of harassment and shooting by hunters for sea lion trimmings or by fisherman (Rowley, 1929). Southeast Farallon Island was inhabited by fair numbers of lighthouse keepers and their families (since the mid-1800s) and egg hunters (men collecting seabird eggs for sale in commercial markets for human consumption) from the mid-1800s to the mid-1900s. Highest human occupancy occurred during World War II, when over 50 military personnel were added to the island's population (Ainley and Lewis, 1974). Families were removed in 1965 and the lighthouse was automated in 1972, after which time only PRBO researchers remained on the island (Ainley and Lewis, 1974). Despite the designation of the North and Middle Farallon Islands in 1909 and the South Farallon Islands in 1969 as a national wildlife refuge, harassment by fisherman and disturbance from low-flying helicopters was common into the 1970s (Ainley and Lewis, 1974). Heightened human presence in the mid-1900s likely increased the abandonment of Steller sea lions from the islands during the period of dramatic decline.

Recent population trends Over the last 20 years, the numbers of Steller sea lions on the South Farallon Islands has continued to decline significantly. Numbers of adult females present during the breeding season declined by 5.9% per year from 1977 to 1996, although the rate of decline has lessened since the mid to late 1980s (Fig. 3B). This rate of decline is much higher than the 3.6% per year decline reported for adult females by Sydeman and Allen (1999), who used maximum counts and data from all seasons, although rates are similar between the two studies when similar data were used (3.2% per year estimated from our study, when data from all seasons were pooled). These findings demonstrate the importance of accounting for seasonal effects when investigating population trends. The rate of decline of 5.9% per year is similar to the rate of decline observed during the breeding season in the area of greatest decline in Alaska (from Kiska Island to the Kenai Peninsula), where rates of decline varied from approximately 5% (1975–85 and 1990–94) to 16% (1985–90; York et al., 1996).

Numbers of immature individuals present during the breeding season have also declined by 4.5% per year over the past several decades, but an overall net increase in immature individuals on the islands has been apparent owing to increased numbers in the late fall and early winter. Numbers of immature individuals on the Farallon Islands in the winter were particularly high from 1984 to 1986. Immature individuals have continued to be present in significant numbers during winter in recent years. It is uncertain where these young animals originated from, but overall declines in juvenile counts, coupled with significant declines in juvenile counts during the breeding season, suggest that increased numbers in winter may represent changes in movement and haulout patterns of juveniles rather than improved juvenile survival in recent years. Increased numbers of subadult males hauled out on the South Farallon Islands during the breeding season in

recent years may have resulted from increased emigration or movement of subadult males from Año Nuevo Island due to increased competition for the declining number of females there. A stable number of adult males, coupled with declines in numbers of adult females, has resulted in a significant reduction in the adult male-to-female ratio on the South Farallon Islands during the breeding season in recent years.

These results demonstrate that reduced numbers of Steller sea lions on the Farallon Islands in recent years have been driven by reduced numbers of adult females during the breeding season, although reproductive rate and pup mortality rate were stable at this peripheral rookery. Patterns were similar at Año Nuevo, where there were sharp declines in numbers of females and pups during the breeding season but where no trend in reproductive rate was apparent from 1962 to 1990 (Le Boeuf et al.[3]). However, unlike the Farallon Islands, number of males at Año Nuevo during the breeding season also declined sharply during the same time period (Le Boeuf et al.[3]). Although the rate of decline at the Farallon Islands has lessened in recent years, large declines of 9.9% per year for pups and 31.5% per year for older animals may have occurred at Año Nuevo from 1990 to 1993, when negative effects of the 1992 El Niño may have affected estimates from this short time series (Westlake et al., 1997).

It is unknown whether reduced numbers of adult females and immature individuals present during the breeding season have resulted from reduced survival or changes in geographic distribution. Because significant declines in Steller sea lions from historical numbers and over the past several decades have occurred at San Miguel Island, Año Nuevo Island, and the South Farallon Islands, greater monitoring and protection by state or federal agencies of the southern populations are warranted. Estimates of age-class specific survival rates of females are needed to determine if reduced numbers of females are due to increased juvenile or adult mortality. More intensive studies tracking individual Steller sea lions in California are required to determine if declining numbers indicate a northward shift in the breeding range and to document migratory movements of males and females. Population dynamics and movements of prey of Steller sea lions, dietary overlap with California sea lions, and interactions of sea lions with commercial fisheries in California must be examined to determine natural and anthropogenic causes for changes in sea lion numbers or distribution.

Acknowledgments

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Larval and settlement periods of the northern searobin (*Prionotus carolinus*) and the striped searobin (*P. evolans*)*

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Abstract—This study reports new information about searobin (*Prionotus* spp.) early life history from samples collected with a Tucker trawl (for planktonic stages) and a beam trawl (for newly settled fish) from the coastal waters of New Jersey. Northern searobin, *Prionotus carolinus*, were much more numerous than striped searobin, *P. evolans*, often by an order of magnitude. Larval *Prionotus* were collected during the period July–October and their densities peaked during September. For both species, notochord flexion was complete at 6–7 mm standard length (SL) and individuals settled at 8–9 mm SL. Flexion occurred as early as 13 days after hatching and settlement occurred as late as 25 days after hatching, according to ages estimated from sagittal microincrements. Both species settled directly in continental shelf habitats without evidence of delayed metamorphosis. Spawning, larval dispersal, or settlement may have occurred within certain estuaries, particularly for *P. evolans*; thus collections from shelf areas alone do not permit estimates of total larval production or settlement rates. Reproductive seasonality of *P. carolinus* and *P. evolans* may vary with respect to latitude and coastal depth. In this study, hatching dates and sizes of age-0 *P. carolinus* varied with respect to depth or distance from the New Jersey shore. Older and larger age-0 individuals were found in deeper waters. These variations in searobin age and size appear to be the combined result of intraspecific variations in searobin reproductive seasonality and the limited capability of searobin eggs and larvae to disperse.

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Although adult fish assemblages offshore of the middle Atlantic states are fairly well known (e.g. Edwards, 1976; Colvocoresses and Musick, 1984; Gabriel, 1992), the early life history of many of these same species and the function of shelf habitats as nursery grounds are poorly understood (e.g. Fahay, 1983, 1993; Able and Fahay, 1998). Because year-class strength is believed to stabilize prior to the early juvenile stage, information about the transition from the plankton to benthic (i.e. settlement) habitats should contribute to our understanding of the population processes of benthic fishes (Cushing and Harris, 1973; Campana et al., 1989; Myers and Cadigan, 1993). Settlement is regarded as a dynamic period of early development because mortality rates can differ between pre- and postsettlement life stages (Sale and Ferrell, 1988), dramatic morphological and physiological transformations occur (Youson, 1988; Markle et al., 1992; McCormick, 1993), and behaviors become evident that allow for delaying settlement until suitable juvenile habitat is found (Cowen, 1991; Sponaugle and Cowen, 1994). Ultimately, an understanding of the life cycle of any benthic species is constrained if the settlement period is not viewed as an integral transition from the planktonic to the adult period.

Our study contributes to an understanding of how fishes use continental shelf habitats as nurseries with an examination of the early life history of the northern searobin, *Prionotus carolinus*, and the striped searobin, *P. evolans*. Both are common species in the coastal region between Cape Cod and Cape Hatteras, but relatively little is known about their early life history owing largely to their low economic importance in relation to the heavily exploited fisheries of this region (McBride et

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al., 1998). Both species are known to begin spawning as early as May and to continue spawning into October as determined by maturity indices (e.g. Richards et al., 1979; Wilk et al., 1990). *Prionotus* spp. eggs and larvae are known to be seasonally abundant above the continental shelf and within some estuaries (e.g. Richards et al., 1979; McBride and Able, 1994) but eggs and larvae are difficult to identify to species on a routine basis. Therefore we took advantage of recently reported morphological information (Able and Fahay, 1998) to examine ichthyoplankton collections.

Our study was designed to examine how spawning patterns varied between two congeners, but intraspecific spawning variation also became evident. A second goal of our study was to examine settlement—to date not reported for either species. Both species undergo flexion and complete fin-ray development at about 6–8 mm SL (Yuschak and Lund, 1984; Yuschak, 1985; Able and Fahay, 1998). Separation of prehensile rays on the pectoral fin, a major adaptation for benthic feeding (Morrill, 1895; Bardach and Case, 1965; Finger and Kakil, 1985), occurs in fish as small as 12 mm SL (Yuschak, 1985). Yet settled juveniles <25 mm SL are rare (Lux and Nichy, 1971; Richards et al., 1979; McBride and Able, 1994), which raises the question of whether *Prionotus* spp. are competent to settle after completing fin-ray development or whether they commonly delay settlement. Using a novel combination of sampling gears, we collected a continuum of late larval and early juvenile *Prionotus* spp. to examine settlement directly. We report for the first time species-specific larval abundances, distributions, ages, sizes, growth rates, and descriptions of early benthic existence.

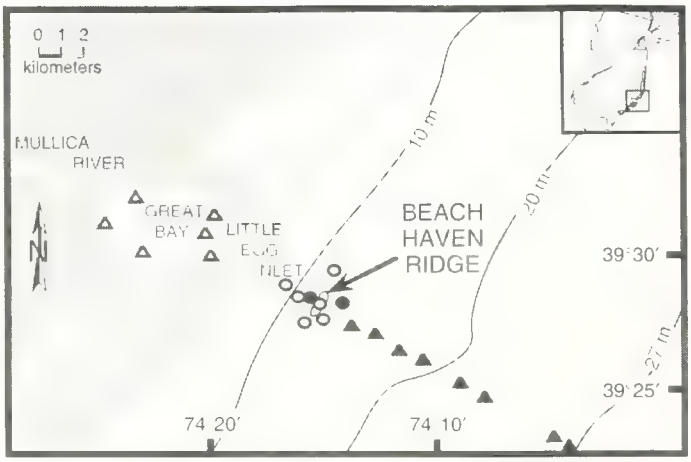

Figure 1

Map of sampling station locations in southern New Jersey, including the main stations at Beach Haven Ridge (landward and seaward; filled circles), other ridge stations (open circles), continental shelf transect stations (filled triangles), and estuarine stations (open triangles). The state of New Jersey, and the study location, are shown in the inset.

Materials and methods

Collections were made in coastal waters of New Jersey, specifically near Beach Haven Ridge (Fig. 1, Table 1), a prominent sand ridge formation that rises to about 8 m depth and is surrounded by depths of 14–16 m (Stahl et al., 1974). Sampling frequency at two stations, one landward and the other seaward of the ridge, was every two to six weeks from July 1991 to November 1992. Two tows of a Tucker trawl (1 m^2) were made at each station in a double, stepped-oblique fashion. One tow was made from the surface to the bottom (three minutes duration) and the other tow was fished from the bottom back to the surface (six minutes). Newly settled juveniles and older fishes were sampled with a 2-m beam trawl in Great Bay estuary, near Beach Haven Ridge, as well as in other habitats (Fig. 1). The data from these stations were arranged in the following groups: 1) the two principal ridge stations (described above); 2) miscellaneous stations scattered on top of and around the ridge; 3) stations along a transect leading directly offshore from the ridge; and 4) a cluster of stations within nearby Great Bay. Generally, three tows were completed at stations immediately landward and seaward of the ridge, but only two tows were completed at other stations. Beam trawl tows offshore of Little Egg Inlet took one minute to complete, but estuarine tows were reduced to 20 or 30 seconds to avoid collecting large volumes of macroalgae, detritus, shell, etc. Sampling occurred during daylight unless otherwise stated. Details of sampling procedures are provided by Hales et al.[1] Volume or area sampled was calculated by using a flow-meter for ichthyoplankton collections or a meter wheel for beam trawl collections. Larval density is presented as the geometric mean number of fish/m^3 for Tucker trawl collections. Juvenile density is presented as the geometric mean number of fish/m^2 of sea bottom. Calculations of geometric means follow Sokal and Rohlf (1981).

The standard length (SL) of all, or at least 20 fish per tow, was measured after the fish were preserved in 95% ETOH. The term "larva" was used in reference to individuals collected in Tucker trawl tows. Preflexion larvae were distinguished from flexion larvae by the absence or presence, respectively, of cartilaginous urals on the ventral edge of the notochord tip; the development of these urals accompanied flexion of the notochord tip (Kendall et al., 1984). Larvae were characterized as postflexion stage once the notochord tip moved anterior to the posterior edge of the hypurals.

Daily age was estimated from counts of sagittal otolith microincrements, which were validated as daily by McBride.[2] Otoliths with a maximum length less than about

[1] Hales, L. S., Jr., R. S. McBride, E. A. Bender, R. L. Hoden, and K. W. Able. 1995. Characterization of non-target invertebrates and substrates from trawl collections during 1991–1992 at Beach Haven Ridge (LEO-15) and adjacent sites in Great Bay and on the inner continental shelf off New Jersey. Technical report (contribution 95-09), 34 p. Institute of Marine and Coastal Sciences, Rutgers, The State University of New Jersey, New Brunswick, NJ.

[2] McBride, R. S. In review. Spawning, growth, and overwintering size of searobins (Triglidae: *Prionotus carolinus* and *P. evolans*).

500 µm were removed and mounted whole on glass slides in immersion oil. Otoliths longer than about 500 µm were mounted in nail polish on a glass slide, sanded with 1500 grit sandpaper along the sagittal plane, and polished with 0.3-µm grinding powder. Immersion oil was used liberally to enhance the clarity of all otoliths, and polarized light aided the viewing of microincrement structure. Microincrement counts were made with a compound microscope, typically at 400×. Slides were coded and microincrements were counted by one reader on three separate occasions. A constant of 4 days, representing the period between hatching and deposition of the first ring, was added to the mean microincrement count to estimate age since hatching (McBride[2]). Preserved (95% ETOH) *P. carolinus* and *P. evolans* were selected in a stratified (0.5-mm intervals), random manner to compare ages and lengths. Microincrement counts from this comparative material ranged, based on all individuals, between 0% and 32% of the mean microincrement count for each otolith (mean=12.0%; n=41).

Prionotus carolinus were collected in far greater numbers than *P. evolans* and they were examined in greater detail. Size and age distributions were initially defined from collections made during the period of peak seasonal abundance (i.e. late September 1991), when a random sample of 34 larvae was selected from a Tucker trawl sample for 23 September. Another sample of juvenile *P. carolinus* was selected from a 2-m beam trawl tow on 23 September 1991 at a station near the above plankton tow (Table 2). Four final samples were selected from 2-m beam trawl tows set one month later (21–22 October) at four stations along a transect of varying depths. Otoliths from all juveniles collected at these stations were analyzed (i.e. only fish that were mutilated or that had cracked otoliths or otoliths sectioned beyond the core were excluded). General methods of measuring and staging individual fish, and preparing otoliths, followed that described above. Sagittal microincrements were counted on two (for larvae) or three (for juveniles) separate dates by one reader. The range of these microincrement counts, for all individuals, was from 0.0% to 25.0% (mean=9.6%; n=127) of each mean count.

Results

Interspecific comparisons

Prionotus carolinus were more numerous and occurred more frequently than *P. evolans* in nearly all collections, typically by an order of magnitude (Table 1). Spawning by both species occurred from at least July to October offshore of southern New Jersey (Fig. 2). Modal size of larvae generally increased with time, but there were exceptions that indicated a pattern of multiple spawning events. For example in August 1991, modal size for *Prionotus* spp. and *P. carolinus* was notably smaller (3–4 mm) than the previous month (5–6 mm) (Fig. 3). Peak larval abundances varied somewhat between years but were highest from July to September.

Prionotus carolinus was the smaller but older congener at each developmental stage. Size and stage were com-

Table 1

Details of plankton and beam trawling data examined in our study. Larvae reported as *Prionotus* spp. were nearly all preflexion stages that did not exhibit diagnostic characters for separating these two congeners. For beam trawl collections, total number of fish are shown at left and the number of age-0 fish are shown to the right (in parentheses). See Figure 1 for general sampling areas.

Sampling area	Tow depth (m)	Net type	Year	Months	Number of cruises	Number of tows	Number of fish collected		
							P. carolinus	*P. evolans*	*Prionotus* spp.
Beach Haven Ridge (landward and seaward only)	0–15	1×1-m Tucker trawl (505-µm mesh)	1991	Jul – Dec	5	21	1274	48	84
			1992	Jan – Nov	14	56	17	0	17
	12–16	2-m beam trawl (6-mm mesh)	1991	Jul – Dec	6	61	459 (403)	40 (32)	0
			1992	Jan – Nov	14	89	122 (79)	26 (18)	0
Other ridge stations	6–17	2-m beam trawl (6-mm mesh)	1991	Aug – Oct	4	22	286 (284)	11 (8)	0
			1992	Jan – Nov	13	46	38 (35)	2 (1)	0
Ridge transect stations	17–24	2-m beam trawl (6-mm mesh)	1991	Oct	1	7	73 (73)	0	0
			1992	Apr – Nov	4	28	114 (111)	0	0
Great Bay	1–4–8	2-m beam trawl (6-mm mesh)	1992	Aug – Oct	3	38	0	1 (1)	0

Table 2

Daily age, size, and hatching dates for planktonic (flexion and postflexion stages) larvae and benthic (settled stage) juveniles of *P. carolinus* collected in September and October 1991, offshore of southern New Jersey (see Fig. 8 for station locations). Data are presented as means (±1 standard error), and the range of values is given in parentheses. Larvae were collected with a 1×1-m Tucker trawl (0.505-mm mesh) and juveniles with a 2-m beam trawl (6-mm mesh).

Date	Stage	Station	*n*	Age (days)	Length (mm)	Hatching date
23 Sep	flexion	OT5	9	15.4 ±0.73 (12–17.5)	5.3 ±0.20 (4.1–6.2)	8 Sep ±0.73 (6 Sep–11 Sep)
23 Sep	postflexion	OT5	25	17.7 ±0.53 (12–23.0)	7.0 ±0.20 (5.7–9.5)	5 Sep ±0.53 (31 Aug–11 Sep)
23 Sep	settled	OT5	23	37.4 ±1.91 24–61.3)	12.2 ±0.44 (8.5–15.8)	17 Aug ±1.91 (24 Jul–30 Aug)
21 Oct	settled	OT2	15	60.9 ±3.06 (46–94.7)	17.5 ±1.42 (12.8–30.4)	19 Aug ±3.06 (18 Jul–5 Sep)
21 Oct	settled	OT5	13	62.2 ±2.81 (52–90.7)	16.8 ±1.58 (12.8–35.3)	20 Aug ±2.81 (22 Jul–30 Aug)
22 Oct	settled	Sta. C	29	75.1 ±2.71 (54–134.0)	21.9 ±1.44 (13.1–59.4)	8 Aug ±2.71 (10 Jun–29 Aug)
22 Oct	settled	Sta. E	13	90.0 ±3.20 (69.3–105.3)	26.3 ±0.96 (20.2–33.7)	24 Jul ±3.20 (8 Jul–13 Aug)

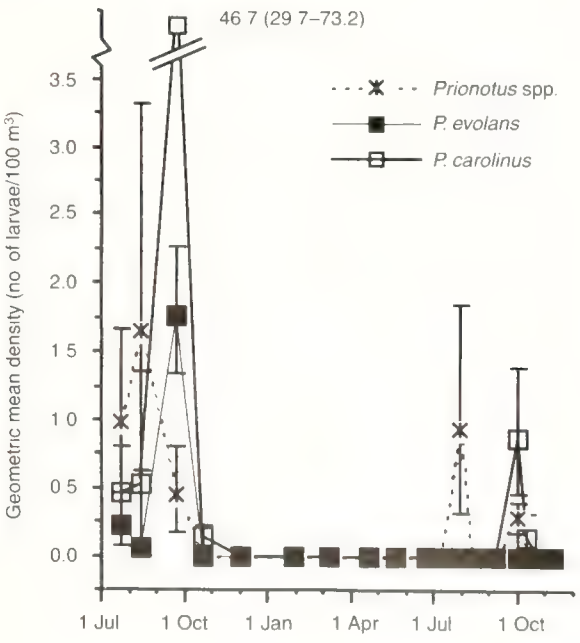

Figure 2

Density (geometric mean number of larvae per 100 m^3 [±1 standard error, SE]) of *Prionotus* spp., *P. carolinus*, and *P. evolans* larvae for each cruise near Beach Haven Ridge, based on daylight tows of a Tucker trawl at the landward and seaward stations (see Fig. 1). Note break in scale (range of SE bars are given in parentheses).

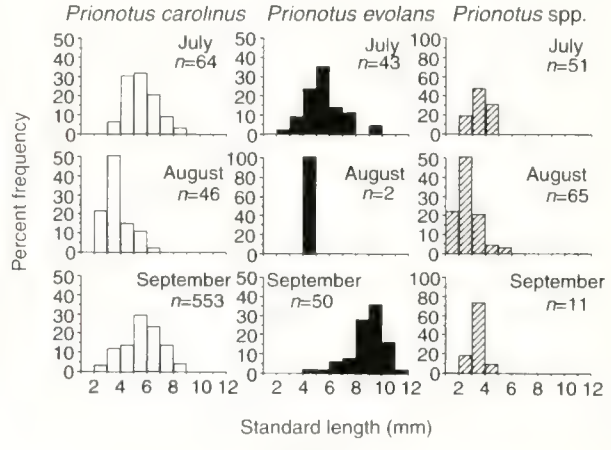

Figure 3

Size frequency of *Prionotus carolinus*, *P. evolans*, and *Prionotus* spp. from Tucker trawl collections near Beach Haven Ridge during July–September 1991. *n* = total number of larvae collected.

pared for 534 *P. carolinus* and 81 *P. evolans* collected with the Tucker trawl during both day and night. Flexion was complete at a larger size for *P. evolans* than for *P. carolinus* (range: 6.7–7.5 mm versus 5.4–6.8 mm SL), and planktonic postflexion *P. evolans* larvae were captured at larger sizes than postflexion *P. carolinus* (range: 6.7–11.9 versus 5.4–9.8 mm SL). *Prionotus evolans* completed flexion at a younger age than *P. carolinus* (approximately 13

versus 18 days after hatching) (Fig. 4). Both species settled as early as 18–19 days after hatching, but this was more characteristic of *P. evolans*; most *P. carolinus* did not settle until 24–25 days old.

Both species grew relatively slowly, and approximately linearly, during the larval and early juvenile period (i.e. ≤0.3 mm/d; Fig. 4, and next subsection). These slow growth rates, combined with the late peak in spawning (i.e. around August), resulted in small body sizes by the onset of winter. These smaller body sizes were particularly true for *P. carolinus*, for which the most pronounced size mode was 10–15 mm SL in autumn 1991 and 1992 (Fig. 5). At this time (i.e. September–December), individuals <50 mm SL constituted 85% of *P. carolinus* and 52% of *P. evolans* from all beam trawl tows combined; during autumn a majority of *Prionotus* spp. were <25 mm SL.

At beam trawl stations, densities of *P. carolinus* were consistently higher than those for *P. evolans* in both 1991 and 1992 (Fig. 6). Geometric mean densities of age-0 *P. carolinus* during the peak period of settlement (September–October) were much higher in 1991 (8.98 fish 100/m^2) than in 1992 (1.56 fish 100/m^2). Geometric mean densities of age-0 *P. evolans* during September–October were also higher in 1991 (0.32 fish 100/m^2) than in 1992 (0.09 fish 100/m^2). These interannual differences were consistent with higher larval densities of both species in 1991 versus 1992 (Fig. 2). Maximum densities of age-0 searobins at a single station reached 28.9 *P. carolinus* 100/m^2 and 3.2 *P. evolans* 100/m^2, both in September 1991. Searobins larger than 150 mm SL were collected infrequently from June to October; occasionally they were found together with age-0 conspecifics in the same beam trawl tows. Age-0 searobins of both species were collected primarily in continental shelf versus estuarine habitats during July–December (Fig. 7).

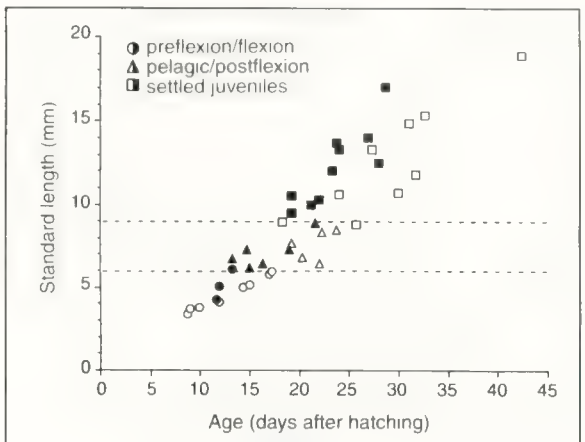

Figure 4

Relationship between daily age and length for *Prionotus carolinus* (open symbols) and *P. evolans* (filled symbols) for preflexion and flexion stages collected with a Tucker trawl (circles), postflexion stages collected with a Tucker trawl (triangles), and settled juveniles collected with a beam trawl (squares). The upper dashed line indicates the approximate size at settlement, and the lower dashed line indicates size at completion of flexion for both species.

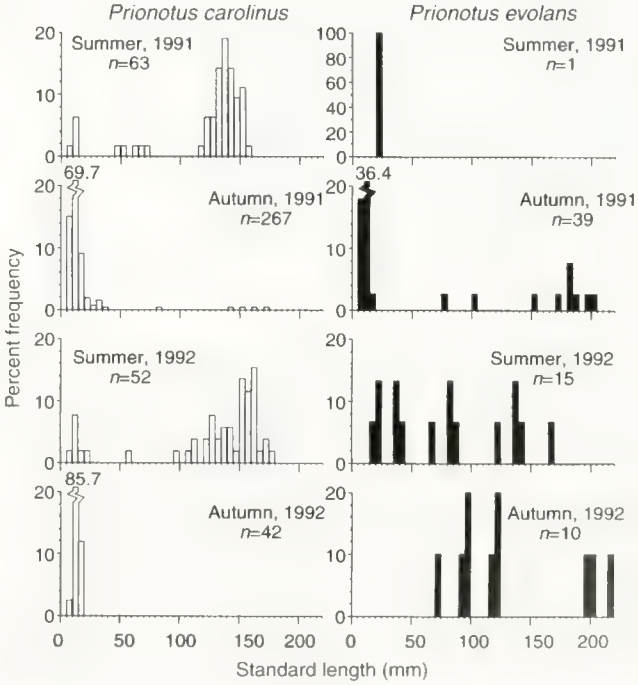

Figure 5

Size frequency of *Prionotus carolinus* and *P. evolans* for beam trawl collections near Beach Haven Ridge (daylight tows at the landward and seaward stations [Fig. 1]). Data were pooled by season: summer (May–August) and autumn (September–December). *n* = total number of fish collected. No data for January–April 1992 are shown because only a single fish (*P. carolinus*; 45 mm SL) was collected at these stations during this period.

Settlement of *Prionotus carolinus*

The seasonality of settlement by *P. carolinus*, although lasting from at least July to October, 1991, was punctuated by a 2–3 week period in September when the vast majority of larvae appeared to settle near Beach Haven Ridge (Fig. 8). Densities of age-0 *P. carolinus* near Beach Haven Ridge were very low during both July and August (geometric means ranging from 0.0 to 1.1 fish 100/m^2). During September, densities increased dramatically (range: 0.8–7.3 and 0.8–28.9 fish 100/m^2 on September 12 and 23–24, respectively). Individuals were collected at all stations along a depth transect, from 6 to 16 m, in late September. Settled, age-0 *P. carolinus* were still widespread and abundant in late October (0.0–13.3 fish 100/m^2), but they were not collected on 2 December 1991, and on 28 January and 10 March 1992.

Collections for 23 September 1991 demonstrate a wide range of *P. carolinus* developmental stages and ages present at Beach Haven Ridge (Fig. 9A). All flexion stages were present (6.5% preflexion, 26.0% flexion, and 67.4% postflexion; *n*=169). Planktonic larvae subsampled randomly from a Tucker trawl tow (*n*=34; Table 2) had hatched during a two-week period from

August 31 to September 11. Individuals collected by beam trawl on the same day (23 September 1991) had hatched about 2 weeks earlier (from 24 July to 30 August) than the above larvae (Fig. 9). These juveniles appeared to settle as young as 24 days after hatching and at sizes as small as 8.5 mm SL (Table 2). The total hatching date distribution for both larvae and newly settled juveniles collected on September 23 reflected a spawning period that ranged from late July to early September and that peaked in late August and early September.

Settled juveniles with a similar hatching date distribution were identifiable one month later at stations near Beach Haven Ridge, but not at stations farther offshore (Fig. 9, B and C). Fish collected near Beach Haven Ridge on 21 October 1991 had a hatching date distribution with a mode from late August through early September and the overall distribution was skewed to the left. This period was similar to the hatching date distributions for larvae and newly settled fish collected on 23 September 1991. In contrast, fish collected from offshore stations (i.e. stations C and E) on 22 October 1991 were 2–4 weeks older and 5–10 mm larger on average (Table 2, Fig. 9).

Plots of *P. carolinus* size versus age did not indicate any abrupt change at settlement, specifically for postflexion larvae and settled juveniles collected on 23 September 1991 (Fig. 10). Growth rates for this September collection fitted a linear model (SL=3.24+0.229[age]; r^2=0.77). Because *Prionotus* larvae hatch at about 3 mm SL (Yuschak, 1985), this model's y-intercept is biologically realistic. Growth rates of fish collected in October did not differ significantly between stations (ANCOVA: $prob._{slopes}$=0.13, $prob._{intercept}$=0.51); therefore the data were pooled. Linear, least squares regression of all data produced an unrealistic y-intercept (SL=–7.01+0.382[age]; SE_a=2.0; r^2=0.74). This model was rerun after restricting the y-intercept to 3 mm and the resulting equation indicated that age-0 *P. carolinus* continued to grow at about 1 mm every 4 days (SL=3 +0.251[age]; r^2=0.65) as they had during the larval and settlement period.

Size and age of *P. carolinus* juveniles varied significantly along a 12-km transect (12–20 m depths; Fig. 1). The linear relationship: $Hatching\ age = 17.8 + 3.43 \times depth$; r^2=0.35, P<0.01; n=69) showed that for every two meters change in depth offshore the fish collected were about one week older on average (Fig. 11). Sampling in both 1991 and 1992 showed a consistent trend for larger (and presumably older) fish to be collected in deeper water in October and November (Fig. 12). After accounting for the effects of depth, or possibly the distance from shore, it appeared that fish reached a larger size in October of 1991 than in 1992 or that larger fish in 1992 were not found in the sampling area.

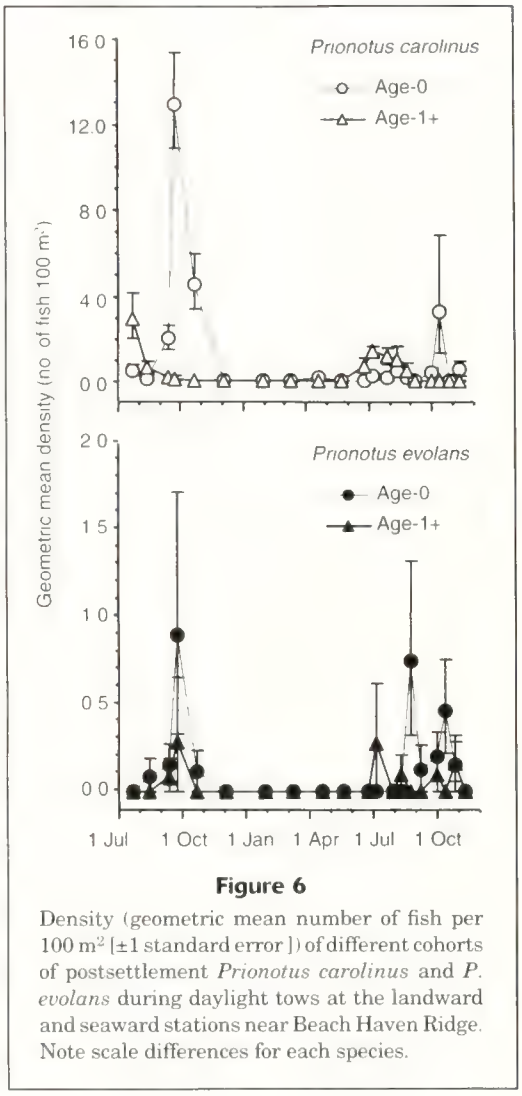

Figure 6

Density (geometric mean number of fish per 100 m^2 [±1 standard error]) of different cohorts of postsettlement *Prionotus carolinus* and *P. evolans* during daylight tows at the landward and seaward stations near Beach Haven Ridge. Note scale differences for each species.

Discussion

Spawning grounds and seasonality of spawning

Prionotus carolinus are more abundant than *P. evolans* in continental shelf habitats whether they are measured as eggs, larvae, juveniles, or adults (Keirans et al., 1986; McBride and Able, 1994; Able and Fahay, 1998; McBride et al., 1998; our present study). The low numbers of *P. evolans* observed in our study may be biased somewhat by our focused effort to sample the continental shelf rather than estuaries. *Prionotus evolans* reside in shallower, warmer habitats than do *P. carolinus* during the spawning season (McBride and Able, 1994). If *P. evolans* spawn to some degree in shallower waters or estuarine habitats, then this would at least partly explain the generally low abundance of *P. evolans* early life stages in our collections.

In general, we expect that larval distributions are good predictors of spawning locations for both *Prionotus* species because of the short (i.e. about three weeks) larval dispersal periods of these species (e.g. Houde and Zastrow [1993] reported several shelf species with planktonic duration >100 days). In some coastal areas, the distribution of *Prionotus* spp. eggs and larvae indicates that spawning may be limited to estuaries; however, the abundance of *Prionotus* larvae offshore of New Jersey suggests that spawning by these species occurs outside estuaries as well. For example, Merriman and Sclar (1952) did not find *Prionotus*

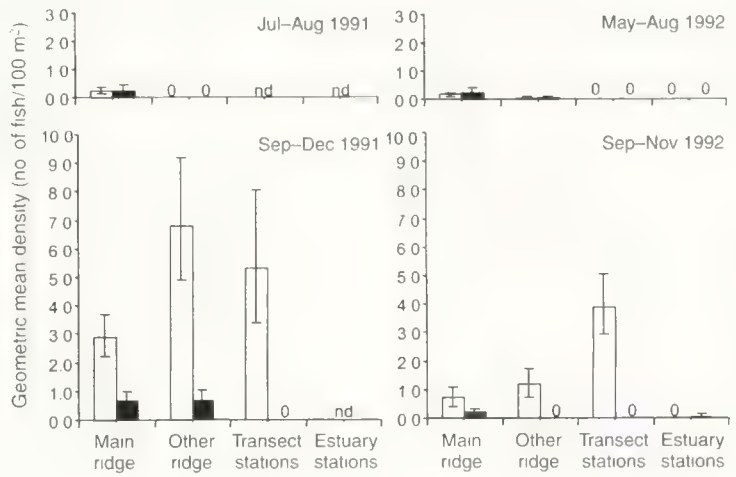

Figure 7

Density (geometric mean number of fish per 100 m^2 [±1 standard error]) of age-0 *Prionotus carolinus* (open bars) and age-0 *P. evolans* (filled bars) collected with a beam trawl from four major station groups (nd= no data; 0=sampling occurred but no *Prionotus* were collected). See Figure 1 and Table 1 for station groupings and locations.

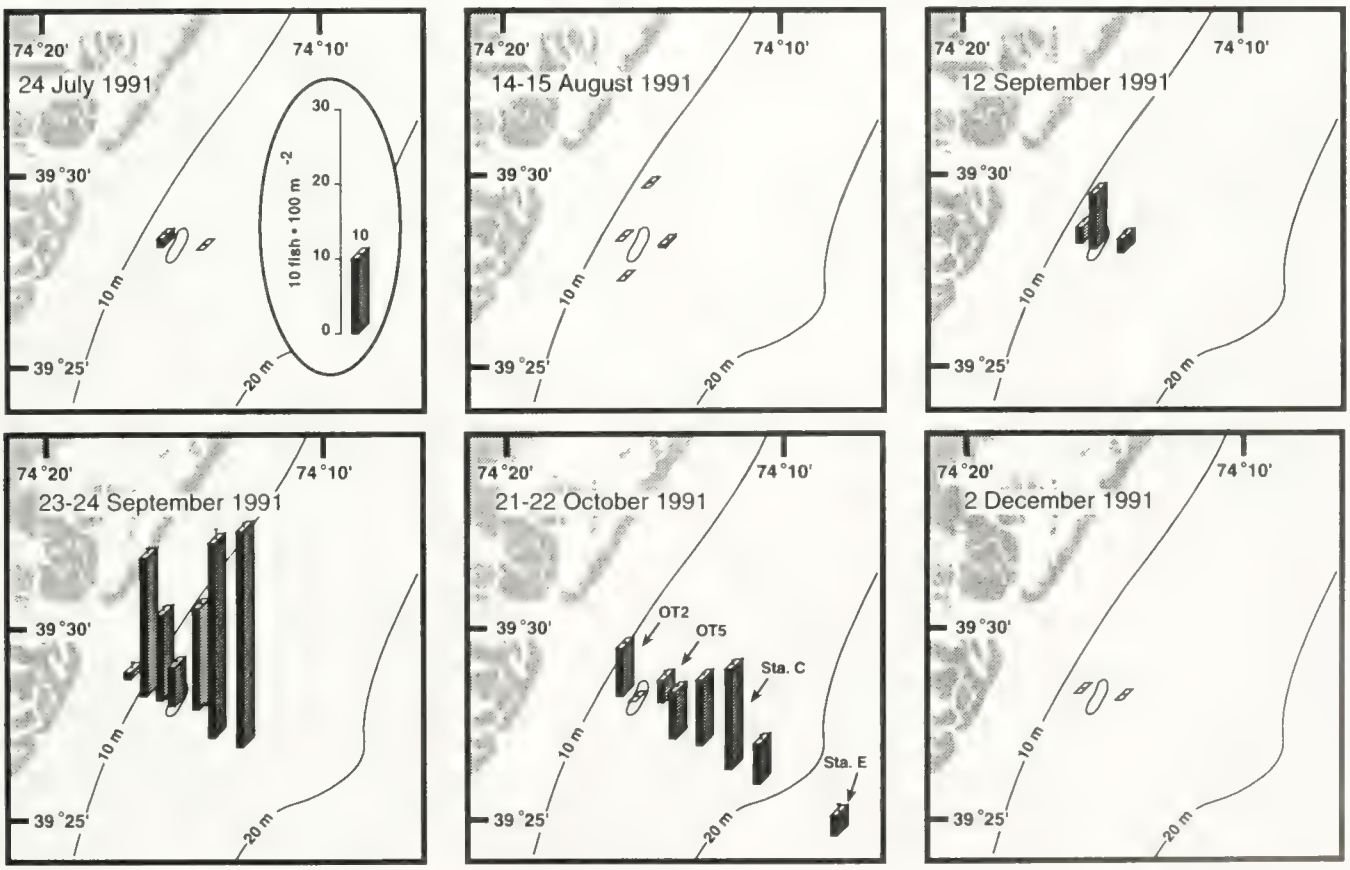

Figure 8

Densities (geometric mean [±1 standard error]) of age-0 *Prionotus carolinus* collected with a beam trawl during six consecutive cruises (July–December 1991). Number of stations varied between cruises. The scale bar indicates 10 fish/100 m^2.

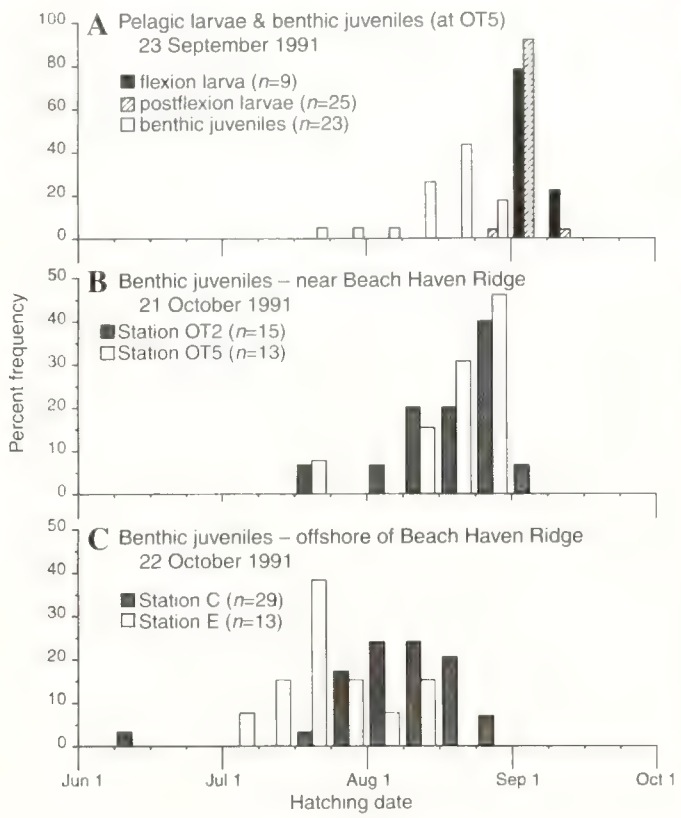

Figure 9

Hatching-date distributions for larval and newly settled juvenile *Prionotus carolinus* collected 23 September 1991 (**A**) and for juveniles collected on 21 October 1991 (**B**) and 22 October 1991 (**C**). See Figures 1 and 8 for locations of sampling stations.

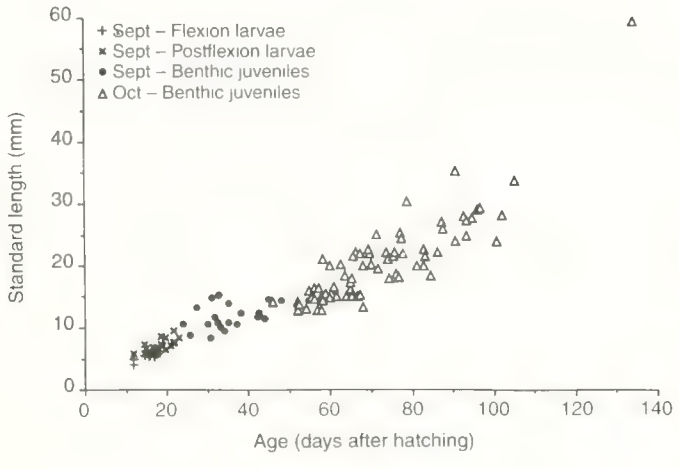

Figure 10

Age (days after hatching) and standard length (mm) for flexion, postflexion, and juvenile *Prionotus carolinus* collected seaward of Beach Haven Ridge on 23 September 1991 and 21–22 October 1991.

spp. eggs or larvae in Block Island Sound, and Able and Fahay (1998) did not observe *Prionotus* larvae above the continental shelf north or east of Hudson Canyon, New York. Instead there are many reports of *Prionotus* eggs, larvae, and juveniles in southern New England estuaries, specifically in Long Island Sound (Wheatland, 1956; Richards, 1959; Williams, 1968; Richards et al., 1979) and Narragansett Bay (Herman, 1963; Bourne and Govoni, 1988; Keller et al., 1999). Thus, the relative importance of estuaries versus shelf habitats as spawning grounds for *Prionotus* may vary in other regions compared with our results for New Jersey. Nonetheless, *Prionotus* spawning seasonality appears to follow a pattern similar to that of other species with a wide latitudinal range that have a shorter spawning season at higher latitudes (e.g. Conover, 1992) and that spawn later in the south (e.g. Barbieri et al., 1994). An important departure from this general trend is that *Prionotus* reproductive seasonality may vary not only with respect to latitude but along an estuary-shelf gradient as well. Because adults of both *Prionotus* species enter estuaries early in the spring and migrate back out to the shelf in summer (McBride and Able, 1994), we postulate that spawning occurs first in estuaries at a given latitude. In support of this hypothesis are the collective results from our study and other published reports. After the summer spawning peak within estuaries such as Chesapeake Bay and Long Island Sound, *Prionotus* spawn during August and September offshore of Chesapeake Bay and New Jersey. In contrast, spawning does not continue into late summer offshore of southern New England (Pearson, 1941; Richards et al., 1979; Able and Fahay, 1998).

To explain this potentially novel spawning pattern does not require any new controlling mechanism other than that used to explain spawning by other coastal fishes of the region. Temperature and photoperiod are known to influence spawning activity in fishes (Burger, 1939) and may influence spawning seasonality of searobins. Water temperatures offshore of the middle Atlantic seaboard are known to fluctuate widely both temporally and spatially (Colvocoresses and Musick, 1984) and this fluctuation affects the spawning pattern of many species. For example, a simple south to north progression of spawning activity above the shelf is evident for *Centropristis striata* (Able et al., 1995) and *Scophthalmus aquosus* (Morse and Able, 1995). For *Prionotus*, however, we propose that spawning seasonality is controlled by an interaction between latitudinal and estuarine gradients of temperature (i.e. earlier spawning in estuaries occurs because of earlier warming of these shallow embayments). Temperature has already been shown to affect the distribution of *Prionotus* adults along both latitudinal and estuarine gradients (McBride and Able, 1994;

McBride et al., 1998). Because few other species use both estuarine and shelf habitats for spawning, such patterns are not commonly observed.

Linking metamorphosis and settlement

Prionotus carolinus are often ranked as among the most abundant species in regional trawling surveys for adult fish or plankton surveys for larval fish (McBride and Able, 1994). The results from the small-mesh beam trawl used in our experiment demonstrate that the juvenile stages of *P. carolinus* are also very abundant offshore. Age-0 *Prionotus* spp. are found in estuaries, as discussed above for the southern New England region, but our observation of high densities of juvenile *Prionotus* in shelf habitats offshore of New Jersey suggest that neither species requires estuarine nursery habitats during their life cycle. Most searobins complete their life cycle in continental shelf habitats (Hoff, 1992), with the notable exception of *P. scitulus* whose young are concentrated in lower salinity, estuarine habitats (Ross, 1978).

Our findings of age and size at settlement largely agree with Yuschak and Lund's (1984) and Yuschak's (1985) descriptions of early development of cultured specimens. The developmental rate of cultured specimens of *P. carolinus* and *P. evolans*[3] did not differ notably from our observations of field-collected individuals, which further supports our conclusion that neither species delays settlement. *Prionotus evolans*, cultured at 20°C, were all at preflexion and flexion stages after 11–13 days; they were at flexion and newly postflexion stages after 18–20 days; and all were at the postflexion stage at 25 days. All available *P. carolinus* specimens, cultured at 15°C, were less than 20 days old; they followed a similar, if slightly slower, rate of development compared with *P. evolans*. Fin-ray development, which greatly facilitates locomotion, is complete in postflexion individuals. Prehensile, chemosensory pectoral rays, which would facilitate benthic feeding, are completely separated by 11.5 mm SL. Thus, on the basis of cultured and field-caught specimens, both species are well developed (i.e. are similar to adults) and well-suited for a bottom-feeding and swimming life style as they complete flexion. Other species delay metamorphosis to settle during favorable lunar phases (Sponaugle and Cowen, 1994), but settlement by *Prionotus* was so concentrated in a single month (i.e. September) that we could not test spawning or settlement cycles in more than one month. Nevertheless, because larvae of *Prionotus* species commonly bury themselves in loose substrate (Bardach and Case, 1965), and this material was common to all our sampling stations (Hales et al.[1]), competent larvae are likely not habitat limited (one mechanism identified with the delay of settlement).

The variation of *P. carolinus* sizes and ages along a depth gradient could be caused by one or a combination of three processes. There could be differential larval survivorship, juvenile movements, or adult reproduction rates

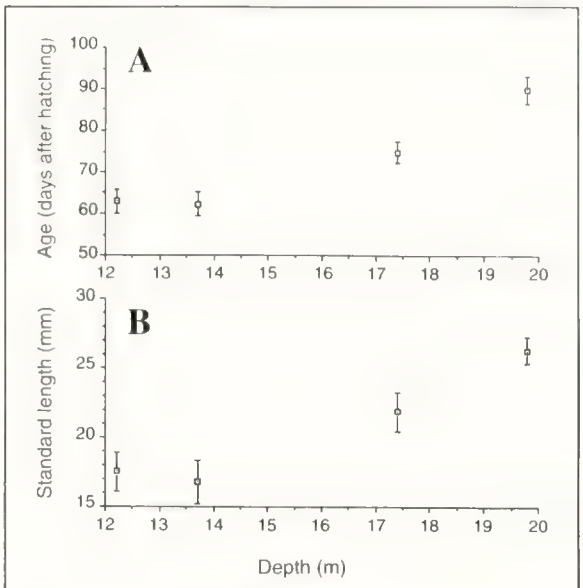

Figure 11

Age (**A**) and size (mean ±1 standard error) (**B**) of juvenile *Prionotus carolinus* plotted in relation to depth. Data are for fish collected on 21–22 October 1991 (near and offshore of Beach Haven Ridge: stations OT2, OT5, C, and E) and aged by using sagittal microincrements (see Table 2 and Fig. 9 for sample sizes).

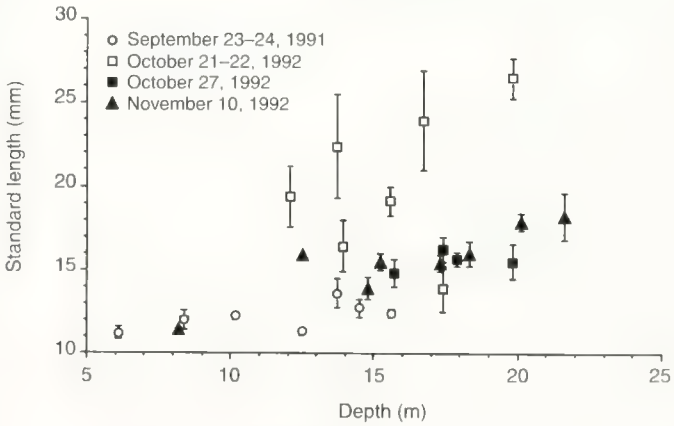

Figure 12

Standard length (mm; mean [±1 standard error]) of juvenile *Prionotus carolinus* in relation to depth for four separate cruises in 1991 (open symbols) and 1992 (filled symbols). All benthic juveniles collected were included in these calculations.

[3] This material was cultured by P. Yuschak (see Yuschak and Lund [1984] and Yuschak [1985]) and has been examined by R.S.M.

across the shelf to account for this spatial pattern of older and larger juveniles farther offshore. The last process was identified earlier as potentially important. Testing and eliminating these hypotheses, however, requires spatially explicit larval distribution data, in addition to the benthic data that we collected, which would allow a comparison of pre-and postsettlement distributions with abundance of *Prionotus* propagules. Spatially explicit environmental data would also be useful because we observed dynamic changes in the physical parameters in our sampling area, and we suspect that these could affect *Prionotus* survival. Vertical stratification of the water column was noted near Beach Haven Ridge on 14 August 1991, but not during cruises in September or October 1991. Low dissolved oxygen levels near the bottom of the ridge, at about 3 ppm (in contrast to >8 ppm in the upper water column) could have negatively affected settlement rates near the ridge in 1991. Stratification near the ridge was also noted in 1992 with similarly depressed levels of dissolved oxygen (Hales et al.[1]). Low dissolved oxygen offshore of New Jersey is not uncommon (Falkowski et al., 1980; Glenn et al., 1996) and may be another process that can contribute to geographic variations in size and age of *Prionotus* species offshore of the middle Atlantic states. We postulate that spatially explicit patterns of reproductive seasonality and age-0 fish size for *P. carolinus* and *P. evolans* within coastal waters offshore of the middle Atlantic states are related to each other because the short planktonic larval durations for both species limit larval dispersal. Interannual variations in water temperature or vertical stratification of oxygen concentrations may be proximate causes for these geographic variations of reproductive seasonality and age-0 size. These patterns could be somewhat unique to searobins, compared with other regional fishes, because searobins use both estuarine and shelf habitats for spawning.

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Abstract—In trawl surveys a cluster of fish are caught at each station, and fish caught together tend to have more similar characteristics, such as length, age, stomach contents etc., than those in the entire population. When this is the case, the effective sample size for estimates of the frequency distribution of a population characteristic can, therefore, be much smaller than the number of fish sampled during a survey. As examples, it is shown that the effective sample size for estimates of length-frequency distributions generated by trawl surveys conducted in the Barents Sea, off Namibia, and off South Africa is on average approximately one fish per tow. Thus many more fish than necessary are measured at each station (location). One way to increase the effective sample size for these surveys and, hence, increase the precision of the length-frequency estimates, is to reduce tow duration and use the time saved to collect samples at more stations.

Assessing the precision of frequency distributions estimated from trawl-survey samples

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Survey-based assessments often appear to provide a more accurate prognosis of the status of a fish stock than catch-based assessments (Nakken, 1998; Pennington and Strømme, 1998; Korsbrekke et al., 2001). An advantage that survey-based assessments have over those based on commercial catch statistics is that the uncertainties associated with survey estimates can be studied and quantified, and based on such research, survey methods, and ultimately stock assessments, can be improved (Godø, 1994). In contrast, it is generally difficult to determine either the accuracy or the precision of estimates based on commercial catch data, and it is not clear how to improve, at a reasonable cost, the collection of catch data so that these data would more accurately reflect the mortality caused by fishing (Christensen, 1996).

Trawl surveys provide estimates of the abundance or relative abundance of a fish stock and estimates of the relative frequency of various population characteristics, such as length, age, and stomach contents. In our study we examined the precision of survey-based estimates of the length-frequency distributions of cod and haddock in the Barents Sea, hake off South Africa, and hake off Namibia. The focus was on length, but the results are relevant for estimating the frequency distribution of other population characteristics.

Materials and methods

Survey length data

Bottom trawl survey length data for Northeast Artic cod (*Gadus mohua*) and Northeast Arctic haddock (*Melanogrammus aeglefinus*)[1] were collected during the Institute of Marine Research (Norway) winter and summer surveys in the Barents Sea. The surveys were stratified systematic surveys and at each station the trawl was towed for 30 minutes.[2]

[1] Also known as "Atlantic cod" and "haddock," respectively, according to *Common and scientific names of fishes from the United States and Canada*. 1991. Am. Fish. Soc. Spec. publ. 20, Besthesda, MD, 183 p.

[2] Aglen, A. 1999. Report on the demersal fish surveys in the Barents Sea and Svalbard area during summer/autumn 1996 and 1997. Unpubl. manuscr., Fisket og Havet NR. 7-1999. Institute of Marine Research, PO Box 1870 Nordnes, N-5817 Bergen, Norway.

The data for the Namibian deepwater hake (*Meluccius paradoxus*) were collected during bottom trawl surveys off Namibia conducted by the Ministry of Fisheries and Marine Resources of Namibia in conjunction with the Norwegian Agency for Foreign Aid (NORAD). For these surveys, tows of 30-minute duration were made at stations along transects perpendicular to the coast.[3]

The data for the deepwater hake for South Africa, were collected from during bottom trawl surveys off the west coast of South Africa. The surveys were conducted by the Marine and Coastal Management Centre, South Africa, by using a stratified random design. Tows of 30-minute duration were made at each station (see Payne et al., 1985).

Assessing the precision of length-frequency estimates

The sample of fish of a particular species measured during a survey is not a random sample of individual fish from the entire population but a sample of n clusters, one cluster from each station. Because fish caught together are usually more similar than those in the general population, a total of M fish collected in n clusters will contain less information about the population length distribution than M fish sampled randomly. One way to measure the information contained in a sample of length measurements is to estimate the number of fish that one would need to sample at random (the effective sample size) to obtain the same information on length contained in the cluster samples.

The effective sample size for cluster sampling can be defined and calculated as follows (Pennington and Vølstad, 1994; Folmer and Pennington, 2000). First estimate the population mean fish length and its variance based on the clusters of fish caught at n stations. Because both the lengths and the number of fish at a station are random variables, a ratio estimator is appropriate (Cochran, 1977). The ratio estimator, $\hat{R}$, of the mean length is given by

$$\hat{R} = \frac{\sum_{i=1}^{n} M_i \hat{\mu}_i}{\sum_{i=1}^{n} M_i}, \tag{1}$$

where M_i = the number of fish caught (either actual or estimated) at station i; and
$\hat{\mu}_i$ = an estimate of the average length of fish at station i.

For example, if the catch at a station is divided into strata and a random sample of fish are chosen in each stratum, then for that station $\hat{\mu}_i$ would be the stratified estimate of mean length. The estimated variance of $\hat{R}$ is approximately given by

$$\mathrm{var}(\hat{R}) = \sum_{i=1}^{n} \frac{(M_i - \overline{M})^2 (\hat{\mu}_i - \hat{R})^2}{n(n-1)}, \tag{2}$$

where $\overline{M} = \sum_{i=1}^{n} M_i / n$.

Next estimate the variance, σ_x^2, of the population length distribution. If m_i fish are randomly selected at each station (or if all fish are measured), then

$$\hat{\sigma}_x^2 = \frac{\sum_{i=1}^{n} \sum_{j=1}^{m_i} (M_i / m_i)(x_{i,j} - \hat{R})^2}{M - 1} \tag{3}$$

is an estimator of σ_x^2,

where $M = \sum_i M_i$ is the total number of fish caught during the survey; and
$x_{i,j}$ = the length of the j^{th} fish at station i.

For other sampling schemes at a station, first estimate the number of fish caught during the survey in each of L length bins, then (e.g. Bhattacharyya and Johnson, 1977)

$$\hat{\sigma}_x^2 = \frac{\sum_{k=1}^{L} f_k (y'_k - \hat{R})^2}{M - 1} \tag{4}$$

is an estimator of σ_x^2,

where f_k = the frequency of fish in the k^{th} length bin; and
y'_k = the bin's midpoint.

Now if it were possible to sample m fish at random from the population, then the variance of the sample mean would be equal to σ_x^2/m. The effective sample, m_{eff}, is defined as the number of fish that would need to be sampled at random so that the sample mean would have the same precision as an estimate based on a sample of n clusters. An estimate of the effective sample size for a particular cluster sample can be derived by substituting the estimates from Equation 2 and either Equation 3 or 4 into the equation

$$\frac{\hat{\sigma}_x^2}{m_{eff}} = \mathrm{var}(\hat{R}). \tag{5}$$

The effective sample size is related to Kish's design effect (*deff*), which for estimating the mean from cluster sampling is defined by (Cochran, 1977)

$$deff = \frac{\mathrm{var}(\hat{R})}{\sigma_x^2 / m}$$

[3] Anonymous. 1999. Survey of fish resources of Namibia. Preliminary cruise report 1/99. NORAD-FAO/UNDP Project GLO92/013, 52. Unpubl. manuscr. NatMIRC, PO Box 912, Swakopmund, Namibia.

Table 1

Summary statistics for assessing the precision of the estimated length distributions of Northeast Arctic cod based on the winter and summer bottom trawl surveys in the Barents Sea. The estimated effective sample size is denoted by $\hat{m}_{eff}$, n is the number of stations at which cod were caught, M is the total number of cod caught, m is the number measured, $\bar{R}$ is the estimate of mean length, and var($\bar{R}$) is its variance.

Year	n	M	m	$\bar{R}$ (cm)	var($\bar{R}$)	$\hat{m}_{eff}$	$\hat{m}_{eff}/n$	($\hat{m}_{eff}/m$) · 100%
Winter								
1995	296	175006	47286	20.0	0.7	313	1.1	0.7
1996	314	209114	44021	18.0	0.3	511	1.6	1.1
1997	177	71418	25689	19.0	2.1	119	0.7	0.7
1998	197	60746	32536	22.1	0.7	394	2.0	1.2
1999	223	50192	21760	25.0	1.9	107	0.5	0.5
	Avg.	113295	34258			289	1.2	0.8
Summer								
1995	329	66643	46161	31.2	1.4	252	0.8	0.6
1996	341	115834	45286	24.4	0.6	478	1.4	1.1
1997	266	72093	26947	23.1	0.8	266	1.0	1.0
1998	218	72360	23461	25.1	1.1	184	0.8	0.8
1999	217	46593	23253	30.8	0.9	211	0.9	0.9
	Avg.	74705	33022			278	1.0	0.9

and, therefore, $m_{eff} = m/deff$. Some statistical software packages for the analysis of complex survey data, such as SUDAAN (Research Triangle Institute, 2001), generate estimates of the design effect.

Simulation techniques were used to examine the effect that reducing the total number of fish measured during a particular survey would have on the estimates of the mean length and the effective sample size. Length measurements consist of one or more subsamples from the fish caught at each station. The simulated estimates of the distributions of $\hat{m}_{eff}$ and $\bar{R}$ (given the actual fish measured during the survey) were generated by randomly selecting from every haul a maximum of k fish without replacement from each subsample. If fewer than k fish were in a subsample, then all were chosen. This was done 500 times for k = 10, 30, and 100, and each run produced values of $\hat{m}_{eff}$ and $\bar{R}$.

To assess the precision of an estimated length distribution, bootstrapping (Efron, 1982) was used to generate 95% confidence intervals for the proportion of fish in each 5-cm length bin. For each of 500 runs, n stations (the number of tows made during the survey) were randomly sampled with replacement and the confidence interval for each 5-cm length bin was based on the resulting 500 estimates of the proportion of fish in that bin. Finally, bootstrapping was used to examine how much the length of the 95% confidence intervals would increase if a maximum of 10 fish were selected from each subsample.

Results

Estimates of the effective sample size and associated statistics for survey-based estimates of the length composition of cod in the Barents Sea are presented in Table 1. The results indicate that for cod the estimated effective sample size is small compared with the number of fish measured. For example during the 1995 winter survey, 175,006 cod were caught, 47,286 were measured, and the effective sample size was 313 fish or 0.7% of the total number measured (Table 1). The average effective sample size for the winter surveys was 1.2 cod per tow and for the summer surveys, 1.0 cod per tow. The estimated effective sample sizes for the Northeast Arctic haddock survey data were, on average, approximately one fish per tow (Table 2).

The effective sample sizes for the survey estimates of the length distribution of deepwater hake off Namibia and off South Africa (Tables 3 and 4) followed the same pattern as for cod and haddock in the Barents Sea. In particular, the average effective sample size was 0.5 hake per tow for the Namibian surveys and 1.3 hake per tow for the South African surveys.

The simulated distributions of $\hat{m}_{eff}$ and $\bar{R}$, which demonstrate the effects of reducing the total number of measured fish on estimates of mean length, for the 1995 and 1999 winter surveys of cod in the Barents Sea are shown in Figures 1 and 2. For example, if a maximum of 30 fish were selected from each subsample at each station, then a total of 11,123 fish would have been measured during the 1995 survey compared with 47,286 fish that were actually measured. For 1995, $\bar{R}$ = 19.96 and the 95% confidence interval for $\bar{R}$ was (18.29, 21.63). As can be seen from Figure 1, all 500 simulated estimates of the mean based on the reduced sample size were well within the 95% confidence limits for $\bar{R}$. When the number of fish measured was reduced to a maximum of 10 fish per subsample for a total sample of 2597 fish, the simulated estimates were also

Table 2

Summary statistics for assessing the precision of the estimated length distributions of Northeast Arctic haddock generated by the winter and summer bottom trawl surveys in the Barents Sea. The notation is the same as that shown in Table 1.

Year	n	M	m	$\hat{R}$(cm)	var($\hat{R}$)	m_{eff}	m_{eff}/m	$(m_{eff}/m) \cdot 100\%$
Winter								
1995	199	66009	22938	25.0	1.0	168	0.8	0.7
1996	235	54892	25525	32.0	2.9	69	0.3	0.3
1997	140	37441	13273	22.0	0.8	185	0.8	1.4
1998	144	12704	9620	23.9	1.0	169	1.2	1.8
1999	182	41612	12152	13.4	0.4	188	1.0	1.6
	Avg.	42532	16702			155	0.8	1.2
Summer								
1995	208	25771	15763	27.0	0.95	147	0.7	0.9
1996	163	14139	7338	31.1	3.65	51	0.3	0.7
1997	114	13560	4314	23.1	1.72	56	0.5	1.3
1998	89	7432	2699	21.3	0.34	170	1.9	6.3
1999	140	11922	5489	20.1	0.36	197	1.4	3.6
	Avg.	14565	7536			124	1.0	2.6

Table 3

Summary statistics for assessing the precision of the estimated length distribution of deepwater hake off Namibia based on bottom trawl surveys. The notation is the same as that shown in Table 1.

Year	n	M	m	$\hat{R}$(cm)	var($\hat{R}$)	m_{eff}	m_{eff}/m	$(m_{eff}/m) \cdot 100\%$
Sep 1990	37	6671	1837	24.6	1.8	35	1.0	1.9
Jan 1991	19	3887	1329	29.2	3.3	19	1.0	1.4
Oct 1992	53	22369	5090	30.1	2.1	30	0.6	0.6
Apr 1992	63	33107	5411	34.0	2.8	30	0.5	0.6
Oct 1993	88	36814	8480	30.3	2.6	41	0.5	0.5
Jan 1993	70	36247	8208	37.3	2.9	33	0.5	0.4
Apr 1993	84	25746	7023	32.7	4.2	35	0.4	0.5
Jan 1994	60	30134	7997	28.4	10.0	13	0.2	0.2
Apr 1994	103	72012	17694	35.3	1.4	63	0.6	0.4
Oct 1994	105	70817	17216	28.1	1.9	44	0.4	0.3
Apr 1995	79	47585	14661	26.0	7.0	20	0.3	0.2
Jan 1996	105	57540	27834	30.3	2.9	45	0.4	0.2
Sep 1996	105	78562	24975	28.7	1.6	50	0.5	0.2
Jan 1997	122	54995	27648	28.5	4.6	29	0.2	0.1
Jan 1998	104	52573	15717	34.5	2.3	44	0.4	0.4
Jan 1999	104	68419	19305	28.4	4.1	30	0.3	0.2
	Avg.	43592	13152			35	0.5	0.5

well within the 95% confidence interval for $\hat{R}$ (Fig. 1). The results of the simulations for the winter survey in 1999 were similar to those for 1995 (Fig. 2).

Bootstrapped estimates of the 95% confidence intervals for the estimated proportion of fish in each 5-cm length bin for the 1995 and 1999 Barents Sea winter survey of cod are shown in Figure 3. The inner brackets denote the confidence interval based on the total number of fish actually measured and the outer brackets denote the confidence intervals if a maximum of 10 fish were measured per subsample.

Discussion and conclusions

For all the surveys examined, the effective sample size for the survey length data was much smaller than the total number of fish measured. The average effective sample size

Table 4

Summary statistics for assessing the precision of the estimated length distribution of deepwater hake off South Africa based on bottom trawl surveys. The notation is the same as that shown in Table 1.

Year	n	M	m	$\hat{R}$(cm)	var($\hat{R}$)	$\hat{m}_{eff}$	$\hat{m}_{eff}/n$	$(\hat{m}_{eff}/m) \times 100\%$
Jan 1985	75	75883	13863	29.3	0.7	70	0.9	0.5
Jul 1985	65	55704	10786	29.9	0.9	52	0.8	0.5
Jan 1986	86	82720	16216	28.2	0.3	132	1.5	0.8
Jan 1987	91	140685	18317	26.7	0.3	122	1.3	0.7
Jul 1987	76	80476	14774	27.0	0.8	68	0.9	0.5
Feb 1988	88	91828	17187	24.3	0.5	98	1.1	0.6
Feb 1989	33	234796	10115	25.7	0.1	207	6.3	2.0
Jan 1990	75	150814	23093	26.0	1.6	43	0.6	0.2
Jan 1991	73	226234	17115	27.2	0.9	38	0.5	0.2
Feb 1992	83	174364	24334	25.2	0.8	58	0.7	0.2
Jan 1993	81	102395	24922	26.0	0.6	89	1.1	0.4
Jan 1994	63	139268	28621	27.1	0.7	68	1.1	0.2
Jan 1995	81	137225	37481	26.4	0.5	97	1.2	0.3
Jan 1996	77	167765	31538	25.2	1.1	46	0.6	0.1
Jan 1997	88	219218	33537	24.2	0.7	70	0.8	0.2
Jan 1998	76	251050	26328	25.9	0.3	116	1.5	0.4
Jan 1999	74	218438	26144	25.4	0.5	91	1.2	0.3
	Avg.	149933	22022			86	1.3	0.5

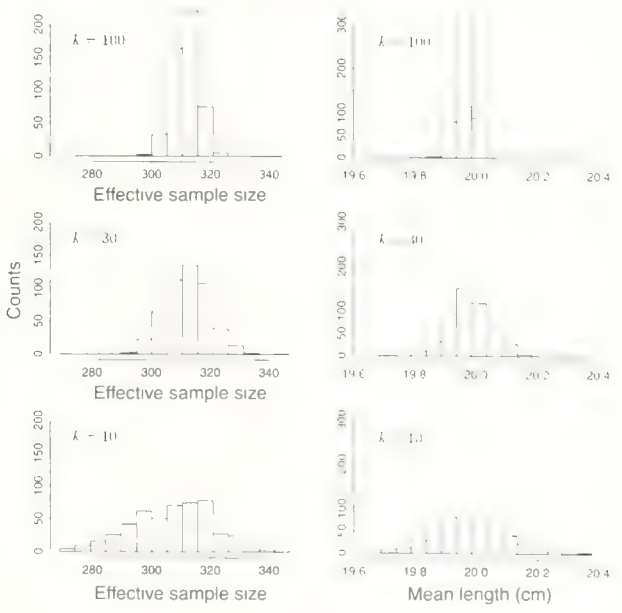

Figure 1

Simulated estimates of the distribution of the effective sample size, $\hat{m}_{eff}$, and of the mean length, $\hat{R}$, when the total number of fish measured is reduced for the 1995 winter survey in the Barents Sea. The top panel is when a maximum of $k = 100$ fish are selected per subsample for a total of $m = 30{,}403$ fish in each run; the middle panel, $k = 30$, $m = 11{,}123$; and the bottom panel, $k = 10$, $m = 3911$. The estimate of the population mean based on the entire sample (m=47,286) is 19.96 and its 95% confidence interval is (18.29, 21.63).

was approximately one fish per tow and it seems to be typical that the effective sample size for estimating length distributions is relatively small for trawl surveys. For example, the effective sample size for trawl surveys of haddock on Georges Bank was on average less than 0.5 fish per tow (Pennington and Vølstad, 1994) and for shrimp in a small area off West Greenland, about 3 shrimp per tow (Folmer and Pennington, 2000).

The reason that the effective sample sizes were small, and, therefore, the estimates of the length distributions were rather imprecise, given the number of fish that were measured, is that the lengths of fish in a haul tend to be more similar than those in the entire population. An additional factor is that the density of fish in a survey region is usually quite variable. To see this, consider the equation for the expected value of var($\hat{R}$). If every fish is measured during a survey, then subject to some assumptions, the expected variance of $\hat{R}$ when n stations are sampled is given approximately by (Pennington and Vølstad, 1994)

$$\mathrm{var}(\hat{R}) = \frac{\sigma_\ell^2\left\{1 + (\overline{M} \quad 1 + \sigma_m^2 / \overline{M})\rho\right\}}{M},$$

where $\overline{M}$ = the expected mean catch per tow;
σ_m^2 = the tow-to-tow variance of catch;
$M(= n\overline{M})$ = the expected total number of fish caught;
σ_ℓ^2 = the population variance of length; and
ρ = the coefficient of intrahaul correlation (see Cochran, 1977, p. 209) for length.

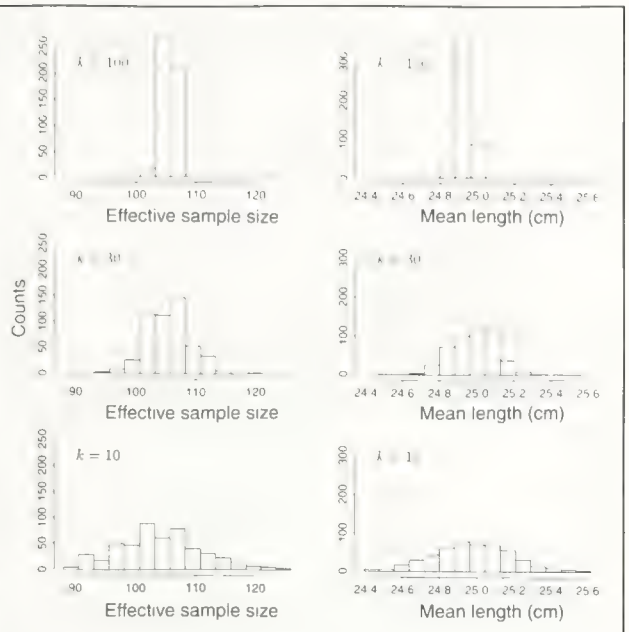

Figure 2

Simulated estimates of the distribution of the effective sample size, $\tilde{m}_{eff}$, and of the mean length, $\hat{R}$, when the total number of fish measured is reduced for the 1999 winter survey in the Barents Sea. The top panel is when a maximum of k = 100 fish are selected per subsample for a total of m = 17,615 fish in each run; the middle panel, k = 30, m = 7240; and the bottom panel, k = 10, m = 2597. The estimate of the population mean based on the entire sample (m=21,769) is 24.96 and its 95% confidence interval is (22.26, 27.66).

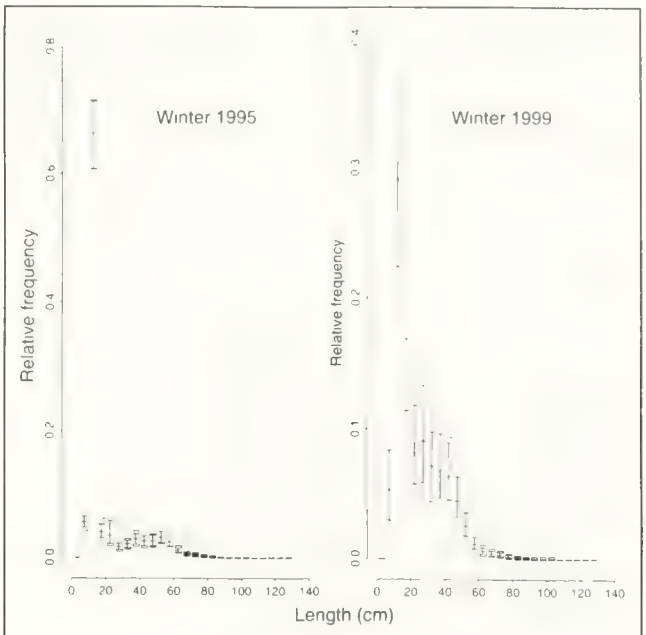

Figure 3

Bootstrapped estimates of the 95% confidence intervals for the proportion of cod in the Barents Sea in each 5-cm length bin, for winter 1995 and for winter 1999. The inner brackets denote the confidence intervals if the estimates are based on all the cod measured during the surveys and the outer brackets denote the confidence intervals if 10 fish are measured for each subsample.

If $\rho = 0$, then $\text{var}(\hat{R}) = \sigma_x^2 / M$ and the effective sample size is equal to M. However if $\rho > 0$ (i.e. fish of similar length tend to be caught together), then the terms in the parentheses can greatly increase the variance and thus drastically reduce the effective size. In particular, the term $\sigma_x^2 / \bar{M}$ is relatively large for trawl surveys. Finally, if $\rho < 0$, which is rarely if ever the case for trawl surveys, then the effective sample size will be larger than M.

The precision of estimates of other population characteristics, such as age distribution, can also be relatively low compared with the number of fish sampled if the particular attribute or measurement is more similar for fish caught together than for those in the general population. For example, the precision of estimates of mean stomach contents (Bogstad et al., 1995) or diet composition (Tirasin and Jørgensen, 1999) can be relatively low because of intrahaul correlation.

An effective sample size of one fish per tow does not mean only one fish should be measured at each station, but it implies that the only way to improve survey precision significantly is to increase the number of stations, i.e. to sample fish from as many locations as possible. The bootstrapped estimates of precision and the sampling simulations showed that reducing or increasing the number of fish measured (or caught and measured) at a station will not significantly affect the precision of length-distribution estimates. In general, if intracluster correlation is positive for an attribute, then it is usually best to take a small sample from as many locations as possible (e.g. Bogstad et al., 1995; McGarvey and Pennington, 2001).

It has been shown that tows of short duration are in general more efficient for estimating stock abundance than long tows (Godø et al., 1990; Pennington and Vølstad, 1991; Gunderson, 1993; Carlsson et al., 2000). Therefore one way to collect samples from more locations and improve overall survey efficiency without increasing survey cost is to reduce tow duration and use the time saved to increase the number of survey stations (Pennington and Vølstad, 1994). For example, if tow duration were reduced from 60 minutes to 15 minutes for a trawl survey of shrimp off West Greenland, then 44% more stations could be surveyed (Carlsson et al., 2000). Likewise, a reduction in tow duration from 30 minutes to 10 minutes for a trawl survey on Georges Bank would increase the number of survey stations by about 30% (Pennington and Vølstad, 1994).

The total number of fish caught would be fewer, on average, if tow duration was reduced, but estimates of fish density would be more precise and the resulting sample of individuals would be more representative of the entire population (Pennington and Vølstad, 1994).

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Estimated ages of red porgy (*Pagrus pagrus*) from fishery-dependent and fishery-independent data and a comparison of growth parameters

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Abstract—The red porgy, *Pagrus pagrus*, is an important reef fish in several offshore fisheries along the southeastern United States. We examined samples from North Carolina through southeast Florida from recreational (headboat) and commercial (hook and line) fisheries, as well as samples from a fishery-independent source. Red porgy attain a maximum age of at least 18 years and 733 mm total length. The weight-length relationship is represented by the ln-ln transformed equation: $W = 8.85 \times 10^{-6}(L)^{3.06}$, where W = whole weight in grams, and L = total length in mm. The von Bertalanffy growth equation fitted to the most recent, back-calculated lengths from all the samples is $L_t = 644(1 - e^{-0.15(t + 0.76)})$. Our study revealed a difference in mean length at age of red porgy from the three sources. Red porgy in fishery-independent collections were smaller at age than specimens examined from fishery-dependent sources. The difference in length-at-age may be related to gear selectivity and have important consequences in the assessment of fish stocks.

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Red porgy, *Pagrus pagrus*, inhabit continental shelves in temperate and tropical waters throughout the Atlantic Ocean and Mediterranean Sea. The species supports fisheries in many countries and is heavily exploited. Since 1992, red porgy has ranked relatively high (38 of 200) in value among all finfish landed commercially in the southeastern United States.[1] Red porgy form a substantial part of overall reef fish landings, especially in North Carolina and South Carolina, although there is little directed fishing for the species. Commercial landings of red porgy from the southeastern U.S. peaked in 1982 at 535 metric tons (t) and declined to 134 t in 1993 (Potts and Burton[2]). Red porgy ranked second by weight for reef fish landed by recreational headboat[3] anglers through the early 1980s. Since then, headboat landings of red porgy have declined, and landings of vermilion snapper, *Rhomboplites aurorubens*, which are also declining, have now surpassed red porgy. White grunt, *Haemulon plumieri*, and gray triggerfish, *Balistes capriscus*, which were less preferred than other members of the snapper grouper complex, have increased in landings and now surpass red porgy.[4]

Mean weight of red porgy from the commercial and recreational fisheries has declined from 1.06 kg in the 1970s to 0.66 kg in 1997.[2] Minimum size regulations (305 mm total length) for recreational and commercial fisheries enacted in 1992 did little to increase mean weight in catches, although the headboat fishery did show a slight increase from 0.48 kg in 1991 and 1992 to 0.60 kg in 1997. Additionally, population biomass estimates for red porgy in the southeastern United States have plummeted from a peak of 3.27×10^6 kg in 1978 to 0.43×10^6 kg in 1992 (Huntsman et al.[5]). These trends suggest that red porgy stocks are being overexploited.

Age determination studies have been conducted throughout the range of red porgy. Manooch and Huntsman (1977) conducted the first comprehensive study using scales (n=1777) and whole otoliths (n=222) to age red porgy that were caught by recreational fishermen using hook-and-line gear off North Carolina and South Carolina when the species was lightly exploited (1972–74). Harris and McGovern (1997) aged red porgy from whole otoliths (n=4281) of

[1] General canvas. 1998. Unpubl. data. Miami Laboratory, National Marine Fisheries Service, 75 Virginia Beach Dr., Miami, Florida 33149.

[2] Potts, J. C., and M. L. Burton. 1999. Trends in catch data for fifteen species of reef fish landed along the southeastern United States. Unpubl. data. South Atlantic Fishery Management Council, 1 Southpark Circle, Charleston, SC 29407.

[3] A "headboat" is a fishing vessel that carries more than six passengers who pay per person (or by the "head") to go offshore fishing.

[4] Headboat annual summaries. 1998. Unpubl. data. Center for Coastal Fisheries and Habitat Research, Beaufort Laboratory, 101 Pivers Island Rd., Beaufort, NC 28516-9722.

[5] Huntsman, G. R., D. S. Vaughan, and J. C. Potts. 1994. Trends in population status of red porgy, *Pagrus pagrus*, in the Atlantic Ocean of North Carolina and South Carolina, USA, 1971–1992. Unpubl. data. South Atlantic Fishery Management Council, 1 Southpark Circle, Charleston, SC 29407.

fish caught from North Carolina to Florida with fishery-independent gear during 1979–81 and 1988–94. Nelson (1988) aged red porgy with scales (n=126) from fish caught in the northwestern Gulf of Mexico with fishery-independent hook-and-line gear and trap gear during 1980–82. In the eastern Gulf of Mexico, Hood and Johnson (2000) aged red porgy from sectioned otoliths (n=852) collected from headboat and commercial catches during 1995–96. Vassilopoulou and Papaconstantinou (1992) used scales from 138 red porgy that were taken with fishery-independent hook and line and trammel nets in the Mediterranean Sea during 1985–86, and Serafim and Krug (1995) aged red porgy from whole otoliths (n=358) that were collected by using commercial longlines and fishery-independent gear in the Azores during 1991–93. Researchers in the Canary Islands aged 1505 red porgy from commercial trap and longline samples during 1985–86 and 1991–93 (Pajuelo and Lorenzo, 1996), and researchers off the Argentinian coast used trawl-caught samples during 1972–81 to obtain 5859 red porgy that were aged from scales (Cotrina and Raimondo, 1997).

Predictions of fish populations from models rely heavily on input data sets, including age and growth. If samples used in the aging study are not representative of the entire population (i.e. the entire geographic range of the stock, full range of fish size, and different gear types), model predictions (e.g. spawning potential ratio [SPR]) can mislead management decisions. A comparative stock assessment of red porgy was done by using growth parameters and age-length keys generated from two studies: 1) fishery-independent data (Harris and McGovern, 1997) and 2) fishery-dependent data (Manooch and Huntsman, 1977; Potts et al.[6]). Each set of age and growth data was applied to fishery-dependent landings and length frequencies. The fishery-independent age and growth data produced a static SPR of 46%, which is well above the overfished definition (SPR<30%) as set forth by the South Atlantic Fishery Management Council (SAFMC). The fishery-dependent age and growth data produced a static SPR of 19% (Potts et al.[6]), which makes red porgy, by definition, overfished and which necessitates that stringent management measures be put in place to protect the stock.

The purpose of our study was to update the age and growth information on red porgy caught in the recreational and commercial fisheries operating along the southeastern United States. We present the von Bertalanffy growth model, weight-length relationship, and age-length keys for red porgy collected from the headboat hook-and-line fishery, commercial hook-and-line fishery, and fishery-independent samples. We also compare mean age at length of red porgy collected from recreational fisheries, commercial fisheries, and fishery-independent sources. We discuss how data source selection affects the growth parameters.

[6] Potts, J. C., M. L. Burton, and C. S. Manooch, III. 1998. Trends in catch data and estimated static SPR values for fifteen species of reef fish landed along the southeastern United States. Unpubl. data. South Atlantic Fishery Management Council, 1 Southpark Circle, Charleston, SC 29417.

Materials and methods

Sagittal otoliths were collected from red porgy landed by hook-and-line fishermen from the headboat (recreational) fishery (n=249) between 1989 and 1998 (59% from 1996 to 1998) and the commercial fishery (n=264) between 1997 and 1998 operating from North Carolina to southeast Florida. From the two fisheries, 64% of the samples came from North Carolina, 14% from South Carolina, and 22% from the east coast of Florida. Because of minimum size limit regulations (305 mm total length), the South Carolina Department of Natural Resources (SCDNR) Marine Monitoring and Prediction (MARMAP) Program supplied us with otoliths from red porgy that were smaller than those available from the fisheries (n=59) and an additional 62 samples ranging from 300 to 425 mm total length. These fish were caught primarily with Chevron traps off South Carolina during 1996 and 1997. Total length, whole weight, port of landing, and date of capture were recorded for each sample. The otoliths were stored dry in coin envelopes.

For age analysis, three transverse (dorsoventral) sections from the left otolith of each fish were taken by using a low-speed saw. One section was made on either side of the core, and the other encompassed the core. The sections were mounted on glass slides with thermal cement, and examined through a microscope at 80× and illuminated with reflected light. Clove oil was applied to each section to enhance the legibility of the growth zones on the section. The samples were put in sequential order from smallest to largest, and one reader counted the number of opaque zones in the otolith section. A second reader examined a random sample of the otoliths. If the readers disagreed on the age of a sample, they examined it again. If consensus was reached, the sample was retained; otherwise, the sample was discarded. Measurements from the core to the outer edge of each successive opaque zone and the otolith margin were taken along the lateral plane on the dorsal lobe of the section by using an ocular micrometer.

Analysis of the marginal increment (the distance between the last opaque zone and otolith margin) was used to validate the annual deposition of the opaque zones in the otoliths. For each age and month, the mean of the relative marginal increment, the ratio of the marginal increment to the distance between the last two opaque zones, was plotted. An opaque zone was considered an annulus if a minimum ratio was recorded for one month or season.

The relationship of fish length and otolith radius was described by regressing the observed total length on otolith radius (R_C). The linear equation was

$$L = a + b(R_C),$$

where L = total length in mm.

The back-calculated total lengths at each age were determined from the body proportional equation (Francis, 1990):

$$L_A = \left[(a + bR_A)/(a + bR_C)\right]L_C,$$

where L_A = back-calculated total length to annulus A;
a = intercept from the linear total length-otolith radius regression;
b = slope from the linear total length-otolith radius regression;
L_C = total length at time of capture;
R_A = otolith radius to annulus A; and
R_C = total otolith radius at time of capture.

The von Bertalanffy equation, $L_t = L_\infty[1 - \exp(-K(t-t_0)]$, was fitted to back-calculated lengths-at-ages for the most recently formed annuli (Ricker, 1975; Everhart et al., 1981; Vaughan and Burton, 1994). Growth parameters were estimated by using SAS PROC NLIN with the Marquardt Option (SAS Institute, 1982) for all aged fish and for fish obtained from fishery-dependent sampling.

Differences in mean back-calculated length at age for the most recently formed annulus for the three sample sources, i.e. recreational, commercial, and fishery-independent, were tested by using the general linear model analysis of variance.

To estimate the whole weight of gutted red porgy landed in the commercial fishery and to estimate stock biomass from assessment models, a regression of ln(*fish weight*) on ln(*fish length*) was performed and transformed to $W = a(L)^b$, where W = weight in g, and L = total length in mm.

Age-length keys were constructed from observed age at length by sample source in which the ages were unadjusted for time of year. Fish that were aged were assigned to 25-mm length intervals.

Results

Red porgy sampled for our study ranged from 176 to 733 mm TL and from 117 to 5895 g in whole weight. Ages were determined for 631 of 634 (99%) sectioned sagittal otoliths. Of those aged, 603 (95%) otoliths were considered legible to record measurements from the core to each successive opaque zone and the otolith margin. On twenty additional samples, we were able to measure only the otolith radius. Sectioned otoliths exhibited a recurrent pattern of alternating wide translucent zones and thin opaque zones. Estimated ages ranged from 1 to 18 years.

Analyses of marginal increment data indicated that the opaque zones were annular in nature and were formed in the spring (Fig. 1). Mean relative marginal increments for ages 2 through 8 were lowest in March through May and were the only months that had marginal increments equal to zero. They then steadily increased from June through October and remained high through February.

Back-calculated total lengths at age of red porgy were estimated from the parameters from the regression equation of total length (L) on otolith radius (R_c). The plot of length on radius was linear, and the linear regression equation that best fitted the data was $L = -132.84 + 10.87(R_c)$ (r^2=0.91, n=623). Using the Francis (1990) body proportional hypothesis, we found that weighted mean back-calculated lengths ranged from 103 mm for age-1 fish to 721 mm for age-18 fish (Table 1).

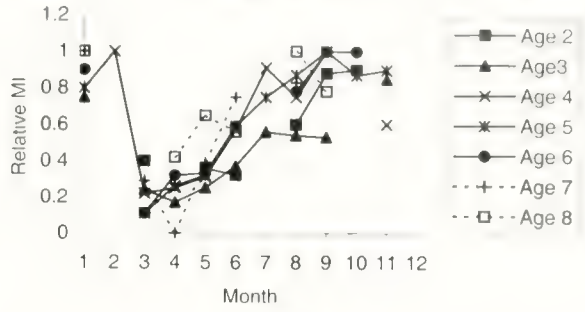

Figure 1

Mean monthly relative marginal increment (MI) of red porgy from the southeastern United States plotted by age.

The back-calculated lengths at the last annulus formation were used to estimate the von Bertalanffy equation. The equation parameters (±1 SE) were L_∞ = 644.72 ±17.93, K = 0.15 ±0.01, and t_0 = –0.76 ±0.10. The theoretical lengths at age ranged from 149 mm at age 1 to 605 mm at age 18. Theoretical lengths closely fitted the observed and back-calculated lengths through age 14 (Table 1). When we used fishery-dependent samples only to generate the von Bertalanffy growth equation, the resulting parameters (±1 SE) were L_∞= 773.73 ±39.49, K = 0.09 ±0.01 and t_0 = –1.96 ±0.21. The fishery-dependent theoretical lengths at age ranged from 181 mm at age 1 to 646 mm at age 18.

We used ages 2 through 6 and data years 1996 through 1998 to compare length at age of the three data sources because the three sets overlapped for those ages and years. The ANOVA on the mean back-calculated length at age of the most recently formed annulus between sample sources indicated a significant difference in age at size between the MARMAP, headboat, and commercial red porgy samples (r^2=0.88; F-value=522.21; P=0.0001 for all combinations) and were represented by the model

$$TL = \alpha_0 + \gamma_C c + \gamma_h h + \sum_{j=1}^{5} \beta_j A_j,$$

where c = 1 if fishery = commercial, or c = 0 if fishery ≠ commercial;
h = 1 if fishery = headboat, or h = 0 if fishery ≠ headboat;
A_1 = 1 if age = 2, or A_1 = 0 if age ≠ 2, etc.; and
j = age categories.

Average $TL = \alpha_0$ for fishery = fishery-independent and age = 6; average $TL = \alpha_0 + \gamma_c c$ for fishery = commercial and age = 6; etc. The model indicated no year effect, and no interaction between fishery and age. MARMAP (fishery-independent) samples were smaller at age than those from the commercial and headboat fisheries. Although mean back-calculated lengths at age between headboat and commercial data sources were statistically different, the differences were slight (<15 mm) (Fig. 2).

Table 1

Mean back-calculated, mean observed, and theoretical total lengths (mm) of red porgy from the southeastern United States.

		Annulus number																	
Age (yr)	*n*	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1	15	134																	
2	33	96	206																
3	136	98	208	274															
4	158	104	212	274	327														
5	136	105	212	274	326	363													
6	56	104	215	275	329	367	399												
7	31	107	216	284	342	381	413	441											
8	26	100	213	278	332	371	400	427	449										
9	6	106	221	283	337	377	410	438	461	483									
10	1	121	221	278	334	379	412	457	491	513	536								
11	2	112	215	275	329	362	395	427	449	476	498	520							
12	1	108	219	274	330	374	407	440	462	485	507	529	551						
14	1	111	226	294	351	385	419	442	465	487	510	533	556	567	579				
18	1	116	247	306	365	413	448	484	506	531	555	567	591	614	638	662	686	709	721
Total	603																		
Weighted mean TL		103	211	275	329	368	404	436	455	489	517	534	566	591	608	662	686	709	721
Incremental growth		103	108	64	54	39	36	32	19	34	28	17	32	25	17	54	24	24	12
Observed TL		198	236	303	350	386	423	459	470	508	547	536	562		590				733
Theoretical TL		149	218	278	329	374	410	443	471	495	516	534	549	562	574	583	592	599	605

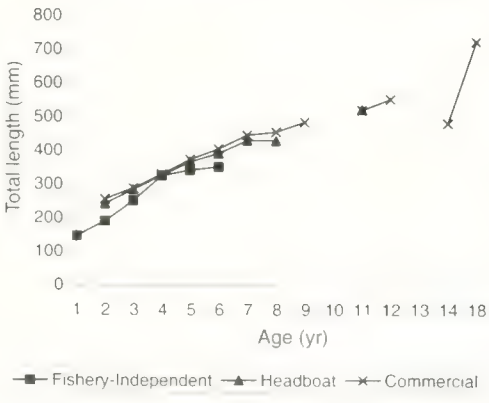

Figure 2

Mean back-calculated length at age of red porgy obtained from a fishery-independent source (MARMAP), headboat operations, and commercial fishery operations between 1996 and 1998.

The weight-length relationship for red porgy in the southeastern United States was best described by the converted ln-ln regression equation of $W = 8.85 \times 10^{-6}(L)^{3.06}$ (r^2=0.96, n=230, MSE=0.01).

Age-length keys by sample source are presented in Table 2. The fishery-independent key is appropriate for fishery-independent length data only. The headboat and commercial keys can be used to convert unaged length samples of red porgy from the fisheries operating in the southeastern United States to aged ones. Annual keys were not available owing to the small sample size from each year.

Discussion

In two previous aging studies on red porgy from the southeastern United States, populations were examined at two different levels of exploitation and different structures were used to determine age. Manooch and Huntsman (1977) sampled recreationally caught fish from an almost virgin stock off North Carolina and South Carolina during 1972–74. Although they used scales and whole otoliths, the main focus of their study and the analysis were on ages determined from scales. Of the 3278 scales analyzed, only 54% (1901) were legible enough to record ages. The main problem of aging red porgy with scales was the large number of regenerated scales.[7] Harris and McGovern (1997) used whole otoliths (n=4281) to age fish collected between 1979 and 1981 and between 1988 and 1994 from the MARMAP survey, a fishery-independent source. The 1988–94 samples in their study came from the area off North Carolina through northeast Florida, although 73% were collected in the area off Charleston, SC, between 32°N and 33°N. The samples were limited mainly to individuals below 450 mm TL (less than 1% of samples were

[7] Manooch, C. S. 1998. Personal commun. NOAA, Center for Coastal Fisheries and Habitat Research, 101 Pivers Island Road, Beaufort, NC 28516.

Table 2

Age-length keys for red porgy from the southeastern United States by sample source: fishery-independent, headboat, and commercial. Total length classes are in 25-mm intervals (i.e. 175 = 175–199).

		Age (yr)																	
TL class	*n*	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Fishery-independent																			
175	11	10	1																
200	21	5	16																
225	7		1	6															
250	9			9															
275	10			10															
300	16			8	6	2													
325	20				11	9													
350	11				5	5	1												
375	14				6	8													
400	1					1													
425																			
450																			
475																			
500																			
525																			
550																			
575																			
725																			
Total	120																		
Headboat																			
175																			
200																			
225	3		3																
250	6		5	1															
275	28		5	23															
300	44			36	7	1													
325	48			15	31	2													
350	41			2	23	16													
375	37				11	21	5												
400	19					11	5	2	1										
425	11					2	5	2	2										
450	5						1	3	1										
475	2							2											
500	3							1		2									
525	2										1	1							
550																			
575																			
725																			
Total	249																		

continued

>450 mm). The data Harris and McGovern presented for the period between 1979 and 1981 showed that 8% of the samples for the reproductive study were greater than 450 mm TL. We sampled from a heavily exploited stock, and fish ranged up to 733 mm TL, and 14% of the fishery-dependent samples were greater than 450 mm TL. Additionally, our samples of red porgy were from a broader geographic range (52% from North Carolina, 30% from South Carolina, assuming all MARMAP samples were from South Carolina, and 18% from east coast Florida) than that of previous studies. Our distribution of samples more closely reflected the landings of red porgy in the southeastern United States. Also, we used sectioned otoliths, which have been determined to be the best struc-

Table 2 (continued)

		Age (yr)																
TL class	*n*	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Commercial																			
175																			
200																			
225																			
250																			
275	5		2	3															
300	25			22	3														
325	34			4	27	3													
350	28				24	4													
375	37				8	24	5												
400	44					29	14		1										
425	27					6	17	3	1										
450	31						7	16	8										
475	20							5	15										
500	7								1	6									
525	1											1							
550	1												1						
575	1														1				
725	1																	1	
Total	262																		

Table 3

Mean observed total length (mm) of red porgy from this study and others: 1 = our study (all data combined); 2 = Manooch and Huntsman (1977: scale data); 3 = Manooch and Huntsman (1977: otolith data); 4 = Harris and McGovern (1997: 1994 data year); 5 = Harris and McGovern (1997: 1988 data year).

	Study				
Age (yr)	1	2	3	4	5
1	198	238	229	218	224
2	236	290	288	294	297
3	303	342	331	306	329
4	350	382	374	328	379
5	386	419	402	344	445
6	423	451	425	362	399
7	459	483	453	386	431
8	470	505	474	374	406
9	508	527	496		448
10	547	543	534	449	
11	536	558	557		
12	562	604			
13		595			
14	590				
15		694			
16					
17					
18	733				

ture to age fish in many studies (Beamish, 1979; Boehlert, 1985; Smale and Punt, 1991).

Red porgy form their opaque zones during the spring along the southeastern United States. Both Manooch and Huntsman (1977) and Harris and McGovern (1997) reported that annulus formation occurred in red porgy during March and April. We found that the opaque zone formed from March through May. Springtime formation has also been reported from the Gulf of Mexico (Nelson, 1988; Hood and Johnson, 2000), from the Azores (May; Serafim and Krug, 1995) and from Argentinian waters (October; Cotrina and Raimondo, 1997). Pajuelo and Lorenzo, in their (1996) study of red porgy off the Canary Islands, found that the opaque zone was formed during the summer (June through October).

A comparison of the mean length at age from our study and that from Harris and McGovern's (1997) study from 1994 (Table 3) clearly reveals that red porgy caught with fishery-independent gear are much smaller at age for fish 3 years and older than fish caught with fishery-dependent gear. Mean size at age in our study was similar to data for fish 5 years and older reported by Manooch and Huntsman (1977) using otoliths, although our mean sizes were smaller that those reported for their scale data. Ages 1–5 of our study were a mix of MARMAP samples and fishery-dependent samples, which may explain why red porgy were smaller for those ages than those reported by Manooch and Huntsman (1977). The mean observed length at age from our study were on average 23 mm smaller than the corresponding lengths from Manooch and Huntsman (1977) for ages 6 through 12 as assigned by scales. The differences may

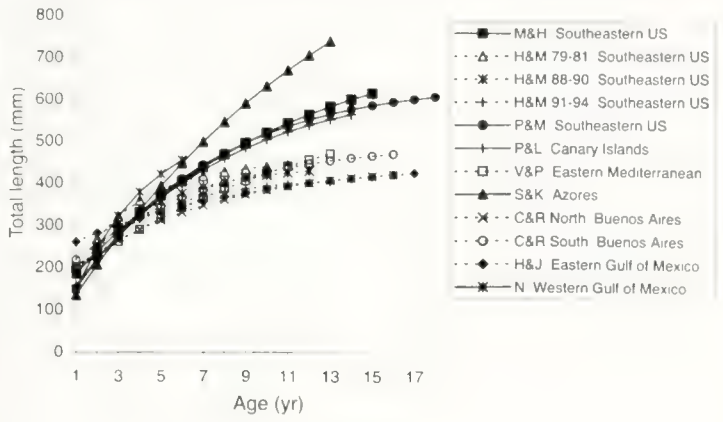

Figure 3

Comparison of von Bertalanffy growth curves from various locations in the Atlantic Ocean: M&H = Manooch and Huntsman (1977); H&M = Harris and McGovern (1997) from three separate data year sets; P&M = Potts and Manooch (this study); P&L = Pajuelo and Lorenzo (1996); V&P = Vassilopoulou and Papaconstantinou (1992); S&K = Serafim and Krug (1995); C&R = Cotrina and Raimondo (1997) from two study areas; H&J = Hood and Johnson (2000); N = Nelson (1988).

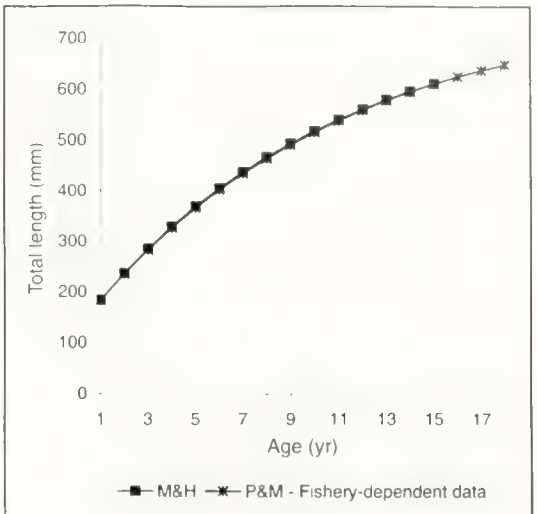

Figure 4

Comparison of the von Bertalanffy growth curve from Manooch and Huntsman (1977) using headboat data versus the resulting growth curves from headboat and commercial fisheries data from this study.

have been due to heavy fishing on the population, the small sample size of older age fish, or differences in assigned ages due to the structure used for aging, because the comparison of ages determined from otoliths was very close.

Harris and McGovern (1997) and Hood and Johnson (2000) have put forth the theory that heavy fishing pressure may cause a shift in the size and age structure of a population to smaller, slower growing fish. Our study does not support this theory. Cotrina and Raimondo (1997) demonstrated the differences in growth of red porgy caught from two areas off Argentina. Because we feel that our samples encompassed the full range of red porgy along the southeastern United States., our data more truly represents that population than the data from Harris and McGovern's (1997) study. We also feel that the perceived changes in length at age reported in Harris and McGovern's (1977) study may be confounded by the changes in sampling strategy of the MARMAP program between 1979 and 1994 (e.g. sampling gear used, locations of sampling, personnel, etc). Differences in growth of red porgy in the Gulf of Mexico between Hood and Johnson's (2000) study and Nelson's (1988) study may certainly be affected by the different locations the samples came from for the two studies. We suggest that further investigation into sample design and effects of habitat, temperature, fishing pressure, weather, fishing gear, etc. on fish populations is needed to help resolve differences between these studies.

The von Bertalanffy growth parameters L_∞ and K are integral components of stock assessment models. Samples for age determination should be representative of the target population (i.e. entire geographic range, all habitats, and all gear types used in the fisheries). Because back-calculated length-at-age information was unavailable to us from all previous studies, we compared the various von Bertalanffy growth curves with direct comparisons of length at age (Fig. 3). The growth curve of red porgy estimated by Manooch and Huntsman (1977), $L_t = 763(1 - e^{-0.096(t + 1.88)})$, is similar to our equation for all samples. Our calculated von Bertalanffy equation with fishery-dependent samples only was almost identical to that of Manooch and Huntsman (1977): $L_t = 774(1 - e^{-0.092(t + 1.96)})$ (Fig. 4). Although aging structures for the two studies were very different, ages were validated in both studies, and overall size ranges were similar.

In comparison with our study and that of Manooch and Huntsman (1977), the growth curves estimated by Harris and McGovern (1997) from their 1979–94 data had L_∞ values ranging from 411 to 451 mm TL. Red porgy in their study exhibited theoretical growth only from 58 to 69 mm, between ages 5 and 11. Red porgy from our study (all data combined) and Manooch and Huntsman's (1977) study theoretically grew from 164 mm to 172 mm, between ages 5 and 11. Also, the growth coefficients (0.27 to 0.34: 1979–94 data) from Harris and McGovern's (1997) data seemed high for red porgy in relation to those reported in other red porgy age and growth studies (Table 4) (Manooch and Huntsman, 1977; Vassilopoulou and Papaconstantinou, 1992; Serafim and Krug, 1995; Pajuelo and Lorenzo, 1996; Cotrina and Raimondo, 1997; Hood and Johnson, 2000).

Studies using fishery-independent sources for red porgy showed smaller L_∞ and higher K values than those from most studies where a combination of commercial, recreational, or fishery-independent samples were used (Table 4). The differences in growth curves are likely a result of smaller fish in the fishery-independent samples and a consequent truncated upper-length range. Although Hood and

Table 4

Comparison of nine age and growth studies of red porgy from the eastern and western Atlantic Ocean. (Rec =recreational fishery, Comm =commercial fishery, F-I=fishery-independent) NC = North Carolina; SC = South Carolina SEFL = southeast Florida; NEFL = northeast Florida. *n* = number of fish in sample.

Study	Location	Aging structure	Age range (yr)	Total length range (mm)	Sample source and *n*	L_∞ (TL, mm)	K	t_0
Manooch and Huntsman (1977)	Southeastern U.S. (NC–SC)	scales	1–15	238–694[1]	Rec *n*=1777	763	0.10	−1.88
Our study	Southeastern U.S. (NC–SEFL)	sectioned otoliths	1–18	176–733	Comm., Rec., and F-I *n*=631	644	0.15	−0.76
Pajuelo and Lorenzo (1996)	Canary Islands	sectioned otoliths	0–14	97–572	Comm. and F-I *n*=1858	640	0.14	0.99
Serafim and Krug (1995)	Azores	whole otoliths	1–13	204–722[1,2]	Comm. and F-I *n*=358	1172–1193[2]	0.06–0.07	−0.70 through −1.70
Hood and Johnson (2000)	Eastern Gulf of Mexico	sectioned otoliths	1–17	194–489	Comm. and Rec *n*=854	459	0.11	−6.6
Harris and McGovern (1997) 1979–94 data	Southeastern U.S. (NC–NEFL)	whole otoliths	1–13	218–449[1,2]	F-I *n*=4281	411–451[2]	0.27–0.34	−0.60 through −1.11
Vassilopoulou and Papaconstantinou (1992)	Eastern Mediterranean Sea	scales	1–13	193–465[1,2]	F-I *n*=151	639[2]	0.08	−3.56
Cotrina and Raimondo (1997)	Buenos Aires, Argentina	scales	0–16	124–480	F-I *n*=5859	447–499	0.15–0.15	−2.96 through −2.81
Nelson (1988)	Western Gulf of Mexico	scales	2–6	302–482[2]	F-I *n*=126	554[2]	0.28	−0.06

[1] Mean total length, actual range of lengths in sample were not readily available.

[2] Fork lengths were converted to total lengths by using $TL = 7.111 + 1.134(FL)$ (MARMAP data, South Carolina Department of Natural Resources, Charleston, SC).

Johnson (2000) used fishery-dependent samples, the largest fish in that study was 489 mm TL, and their samples came from primarily one location. Selectivity of fishing gear may also explain differences in growth parameters. For example, hook-and-line gear may catch faster growing and more aggressive fish, whereas traps and trawls may catch slower growing fish and overall smaller fish. We recommend that in future age and growth studies of any fish species, samples represent the full range of fish sizes in a population, including fish caught by many different gear types, and are obtained from the entire geographic range of the stock. Where practical, landings should be stratified and sampled accordingly.

Acknowledgments

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Bycatch in the tuna purse-seine fisheries of the western Indian Ocean

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Abstract—Bycatch taken by the tuna purse-seine fishery from the Indian Ocean pelagic ecosystem was estimated from data collected by scientific observers aboard Soviet purse seiners in the western Indian Ocean (WIO) during 1986–92. A total of 494 sets on free-swimming schools, whale-shark-associated schools, whale-associated schools, and log-associated schools were analyzed. More than 40 fish species and other marine animals were recorded. Among them only two species, yellowfin and skipjack tunas, were target species. Average levels of bycatch were 0.518 metric tons (t) per set, and 27.1 t per 1000 t of target species. The total annual purse-seine catch of yellowfin and skipjack tunas by principal fishing nations in the WIO during 1985–94 was 118,000–277,000 t. Nonrecorded annual bycatch for this period was estimated at 944–2270 t of pelagic oceanic sharks, 720–1877 t of rainbow runners, 705–1836 t of dolphinfishes, 507–1322 t of triggerfishes, 113–294 t of wahoo, 104–251 t of billfishes, 53–112 t of mobulas and mantas, 35–89 t of mackerel scad, 9–24 t of barracudas, and 67–174 t of other fishes. In addition, turtle bycatch and whale mortalities may have occurred. Because the bycatches were not recorded by some purse-seine vessels, it was not possible to assess the full impact of the fisheries on the pelagic ecosystem of the Indian Ocean. The first step to solving this problem is for the Indian Ocean Tuna Commission to establish a program in which scientific observers are placed on board tuna purse-seine and longline vessels fishing in the WIO.

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One of the most important requirements of the UN Convention on the Law of the Sea of 1982, which determines strategies for exploitation of marine living resources (Article 119, b), is to take into account the impact of fisheries on ". . . species associated with or dependent upon harvested species with a view to maintaining or restoring populations of such associated or dependent species above levels at which their reproduction may become seriously threatened. . ." (United Nations, 1983). Estimating the magnitude of bycatch is one of the first steps to determine the impact of fisheries on associated species.

Tuna purse-seine fisheries probably apply the most intensive direct human impact on the tropical epipelagic ecosystems in all oceans. Because of the worldwide scale of purse-seine fisheries, an assessment of their impact on associated and dependent species is essential.

Two tunas, yellowfin *Thunnus albacares* (Bonnaterre, 1788) and skipjack *Katsuwonus pelamis* (Linnaeus, 1758), are the target species of most purse-seine fisheries. In this study bycatch is defined as the fraction of the catch that consists of nontarget species (including other species of tuna) that are encircled by the fishing gear and are unable to escape by themselves. Bycatch of associated and nonassociated species during purse-seine fishing for tropical tunas may be rather high, and generally depends on fishing tactics.

The species composition of bycatch in purse-seine fisheries depends on the structure, behavior, and spatial organization of surface multispecies aggregations. Schools of different tuna species and other pelagic fishes, marine mammals, and other marine animals have aggregated distributions. From our observations and in the opinion of other researchers (Au and Perryman, 1985; Au and Pitman, 1986; Au, 1991; Cort, 1992), marine birds are also an integral component of the majority of these multispecies groups.

The tunas, as a rule, prevail by biomass and abundance in such groups. Tuna schools are traditionally classified by the visually distinctive part of the group or by whether they associate with floating objects or marine mammals (Scott, 1969; Petit and Stretta, 1989). "Free-swimming schools" may include associations between different species of tuna. For each type of school, its various components occur in different ratios.

Some epipelagic species that occur in the purse-seine bycatches are not members of multispecies aggregations. They, instead, may comprise members of the flotsam community or are tuna forage. Several associated components, such as whales and birds, usually escape or avoid the nets and do not become bycatch. Therefore, the composition of the catch often does not represent the actual species composition of the multispecies associations.

Assessments of bycatches have been made for the eastern Pacific Ocean purse-seine tuna fishery (Joseph, 1994; Garcia and Hall, 1995; Hall, 1996, 1998; Anonymous, 1997, 1998, 1999), where the bycatch problem attracted attention because of dolphin mortality during sets on dolphin-associated tuna schools. The economic, political, and ecological implications of this problem produced wide international attention (Charat-Levy, 1991; Joseph, 1991, 1994; Hall, 1998). Bycatch estimates for the western Pacific purse-seine tuna fisheries have been published also (Bailey et al., 1996).

In the western Indian Ocean (WIO), tuna-dolphin associations are well known in coastal pelagic zones, e.g. Gulf of Aden (Demidov[1]) and Sri-Lanka (de Silva and Boniface[2]). They are often used in small-scale troll and pole-and-line fisheries for locating yellowfin tuna. In offshore regions of the WIO tuna-dolphin associations are rare, purse seining for them is not practiced, and there is no dolphin bycatch problem. Perhaps for this reason, the magnitude of bycatch in the WIO is unknown, except for recent information on species composition (Santana et al., 1998). Bycatches are not recorded for tuna seiners operating in the WIO, except bycatches of nontarget tuna species. This paper represents a first attempt to estimate catches of associated species by tuna purse seiners in the WIO, based on scarce information collected by scientific observers.

Materials and methods

Bycatch assessments were based on data collected by YugNIRO scientific observers aboard Soviet (since 1992—Russian) tuna purse seiners in the WIO, during 1987, and 1990–91. The vessels were the "Rodina" type.[3] In addition, observer data collected in the same area aboard sisterships by AtlantNIRO[4] and "Zaprybpromrazvedka"[5] during 1986–90 and data by TINRO[6] and TURNIF[7] during 1990 and 1992 were used. The fishing vessels all used purse seines of 1800 m in length, 250–280 m in depth, and 90–100 mm mesh size in the bunt.

The principal goal of the observer sampling program was an estimation of the species composition of catches in this fisheries, biological analysis of the principal species, and estimates of the length and weight compositions of these principal species in the catches. The observers were placed on board opportunistically (i.e. if a vessel had a free sleeping bed and if there was available funding), without a sampling scheme and without preference to any vessel type. Thus, the sampling could be considered as random. Two other types of Soviet fishing vessels, "Tibiya"[8] and "Kauri,"[9] which took part in the Indian Ocean fisheries during 1985–87 and since 1991 (under the Liberian flag), were not sampled. In this study coverage rate was estimated as percentage of sampled catch to total catch.

The observers recorded the results of each set. The type of school, according to Scott (1969) and Petit and Stretta (1989), of each set was recorded. I considered sets for which an observer recorded catch in any quantity as positive sets. The average bycatch level was estimated for all positive sets.

For the positive sets, species composition, total weights, and numbers of each species in the catch were recorded. In the vessels of the "Rodina" type, the retained catch was frozen and stored separately. The retained catch was weighed after freezing while being moved to the ship's holds. In nine cases, the weight of some of the catch was estimated by the ship masters because the holds were overloaded and some catch was stored in the freezers till landing. Therfore estimates of retained catch are presented in this study as frozen weights rather than wet weights. The bycatch was estimated as wet weight. Only bycatch taken on board was sampled. The sets when bycatch was not taken onboard but discarded alive (usually with negligible target species catch) and malfunction sets, which do not produce any catch, were not analyzed in this study. Large species, sharks and billfishes generally, were weighed and counted. The weights of specimens heavier than 200 kg (i.e. Mobulidae) were estimated. When the bycatch was more than 200–300 kg, species composition and weight were estimated by using representative samples.

Sometimes the observer recorded the bycatch in numbers. In these rare cases, the total weights of the fishes were estimated from the average weights of these species in previous catches.

The observers had free access to every fish in the catch. Nevertheless, some observers had difficulties identifying some billfishes, sharks, and Mobulidae species. Therefore, I pooled the records with doubtful species identification into these three groups for my analysis. These are marked by "?" in the tables.

The data were grouped and analyzed by free-swimming schools (including associations between schools of different species of tuna) and associated schools. The latter included whale-associated schools and log-associated schools (associated with floating objects).

Schools caught in the area of seamounts and shoals—at the peaks of the Equator Seamount and at Saya-de-Malha bank—were considered free-swimming schools. Some observers did not record the type of floating objects that were set on; therefore the sets on natural floating objects (50% to 90% of the log sets sampled) and on fish aggregation devices (FADs) (10–50%) were grouped. Several log sets were made in areas with surface evidence of water masses or current interactions (rips). A set that could not be clearly identified as to set type was made in such an area and was treated as a log set because of the species composition of the catch and the occurrence of small scattered debris in the rips.

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[1] Demidov, V. F. 1998. Personal commun. Southern Scientific Research Institute of Marine Fisheries and Oceanography (YugNIRO), 2, Sverdlov St., 98300, Kerch, Crimea Ukraine.

[2] de Silva, J., and B. Boniface. 1991. The study of the handline fishery on the west coast of Sri Lanka with special reference to the use of dolphin for locating yellowfin tuna (*Thunnus albacares*). *In* Indo-Pacific Tuna Development and Management Programme (IPTP) Coll. Vol. Work. Doc TWS/90/18., Vol. 4, p. 314–324. Food and Agriculture Organization of the United Nations (FAO), Viale delle Terme di Caracalla, 00100, Rome, Italy.

[3] Length overall: 85 m; GRT (gross tonnage): 2634; carrying capacity: ~1600 m^3.

[4] AtlantNIRO—The Atlantic Scientific Research Institute of Marine Fisheries and Oceanography, 5 Dmitry Donskoi St., 236000 Kaliningrad, Russia.

[5] The Department of Searching and Scientific Research Fleet of the Western Basin "Zaprybpromrazvedka," 5[a] Dmitry Donskoi St., 236000 Kaliningrad, Russia.

[6] TINRO—The Pacific Scientific Research Institute of Marine Fisheries and Oceanography, 1 Shevchenko Alley, 690600 Vladivostok, Russia.

[7] TURNIF—The Pacific Department of Fish Searching and Scientific Research Fleet, 2 Pervogo Maya St., 690600 Vladivostok, Russia.

[8] Length overall: 55.5 m, GRT: 736, carrying capacity: ~361 m^3.

[9] Length overall: 79.8 m, GRT: 2100, carrying capacity: ~1200 m^3.

Table 1

Numbers of sets sampled by year. Positive sets are sets in which an observer registered catch in any quantity .

	1986	1987	1988	1989	1990	1991	1992	Total
Total number of sets	115	102	30	41	113	54	39	494
Number of positive sets	68	62	28	41	92	53	33	377
Percentage of sets with catch	59%	63%	93%	100%	81%	98%	85%	76%

Table 2

Numbers of sets sampled by season and type of school.

	Seasons				
Type of school	Winter	Spring	Summer	Autumn	Total/positive
Free-swimming	136	35	27	8	206/121
Whale-shark–associated	2	0	0	0	2/2
Whale-associated	23	21	1	0	45/37
Log-associated	46	50	80	65	241/217
Total	207	106	108	73	494/377

Because tuna purse-seine fishing in the WIO is clearly seasonal (monsoons governing fishing techniques and operations), the data were analyzed by season. I followed Romanov's (1982) seasonal divisions, in accordance with long-term average seasonal variations in the monsoon atmospheric circulation for the WIO. The winter season (northeastern monsoon) lasts from December to March, the spring intermonsoon period falls during April and May, the summer (southwestern monsoon) lasts from June to August, and the autumn intermonsoon period lasts from September through November. The wind regime determines the onset and duration of the hydrological seasons, which do not quite coincide with seasons of atmospheric circulation owing to a considerable time lag of the processes occurring in the ocean. However, the wind regime is instrumental in determining the tactics of purse seining for tuna; therefore I used seasonal strata based on atmospheric rather than on hydrological processes.

The spatial and temporal distribution of catch and effort for the Soviet tuna purse-seine fishery in the Indian Ocean was determined from data in the YugNIRO database, a collection of daily radio reports from vessels fishing in the area from 1983 until the mid-1990s.[10] The catches reported by the author's estimates varied by 96–99% during 1985–91, decreasing to 71% in 1992. This study did not take into account reflagging of some Soviet (from 1992—Russian) vessels with the Liberian flag, and the vessels' nationality was defined in this study by the location of their shipowners. Analysis of fleet activity and extrapolations of results were made on the assumption that the operations and procedures on vessels that did not carry observers did not differ from the operations and procedures on vessels with an observer aboard; similarly it was assumed that the species composition of the catch from these vessels did not differ.

Some of the bycatch was retained on board the fishing vessels. Unused bycatch was discarded in the ocean. The observers usually did not record the levels of discards, and it was not possible to assess quantitatively the discards of tuna and associated species.

Average values are presented as arithmetic means, plus or minus 95% confidence intervals for estimated values. Estimates of unrecorded bycatches for all fishes, except tunas, are provided in numbers and metric tons per positive set and per 1000 t of target species.

Results

Primary data and adequacy of samples

A total of 494 purse-seine sets were sampled and 377 positive sets were analyzed. The total catch in the sets that were sampled amounted to 7713 t. The distribution of sets sampled by years, seasons, and the types of schools is given in Tables 1 and 2. The catch sampled by type of school is presented in Table 3.

The observer coverage rate varied from 0% (no observers at sea) to 75% and averaged 14% during 1986–92. During the periods when observers were on board, the coverage rate averaged 30% and varied from 5% to 75%. The spatial distribution of sampled sets agreed quite well with

[10] Daily information on fishing activity of these vessels in the Indian Ocean in 1983–84 and since 1995 is not available.

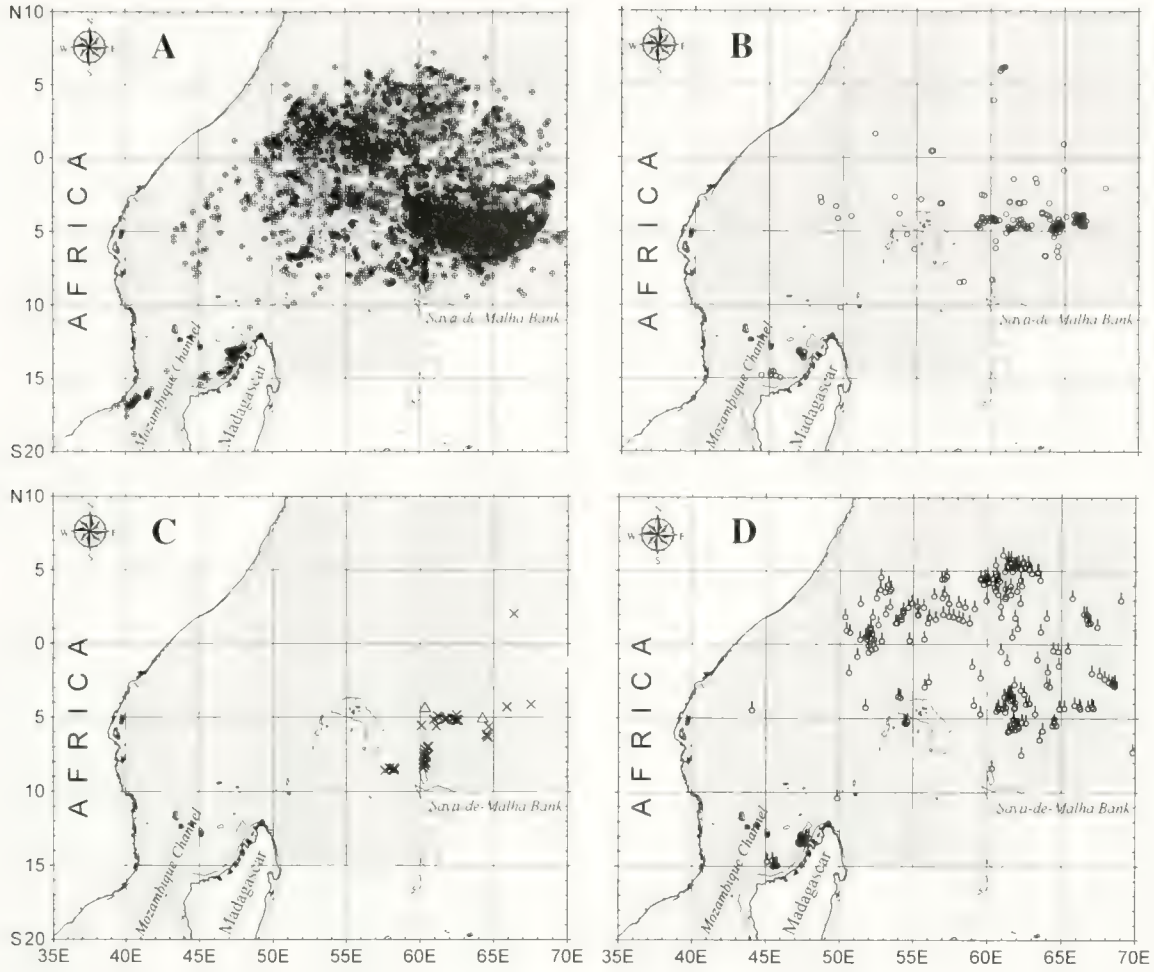

Figure 1

(A) Fishing effort distribution (⊗=noon positions of vessels on fishing days with sets) of the Soviet tuna purse-seine fishery in 1985–94; **(B–D)** sampled set positions: (B) on free-swimming schools that were sampled; (C) on whale-shark (△) and whale-associated schools (×); (D) on log-associated schools. The shaded area represents the region of the main international tuna purse-seine fishing activity in the WIO, according to Ardill.[11]

Table 3

Sampled catch (metric tons) by season and type of school.

	Seasons				
Type of school	Winter	Spring	Summer	Autumn	Total
Free-swimming	1884	249	73	24	2230
Whale-shark–associated	28	0	0	0	28
Whale-associated	584	467	4	0	1055
Log-associated	925	785	1156	1534	4400
Total	3421	1501	1213	1558	7713

the distribution of the total fishing effort of the Soviet fleet in the WIO (Fig. 1). Sampled sets were distributed throughout the region of the principal international tuna purse-seine fishing activity in the WIO (Ardill[11]). Thus, I

[11] Ardill, J. D. 1995. Atlas of industrial tuna fisheries in the Indian Ocean (IPTP/95/AT/3). IPTP, Colombo, Sri Lanka, 138 p. FAO, Viale delle Terme di Caracalla, 00100, Rome, Italy.

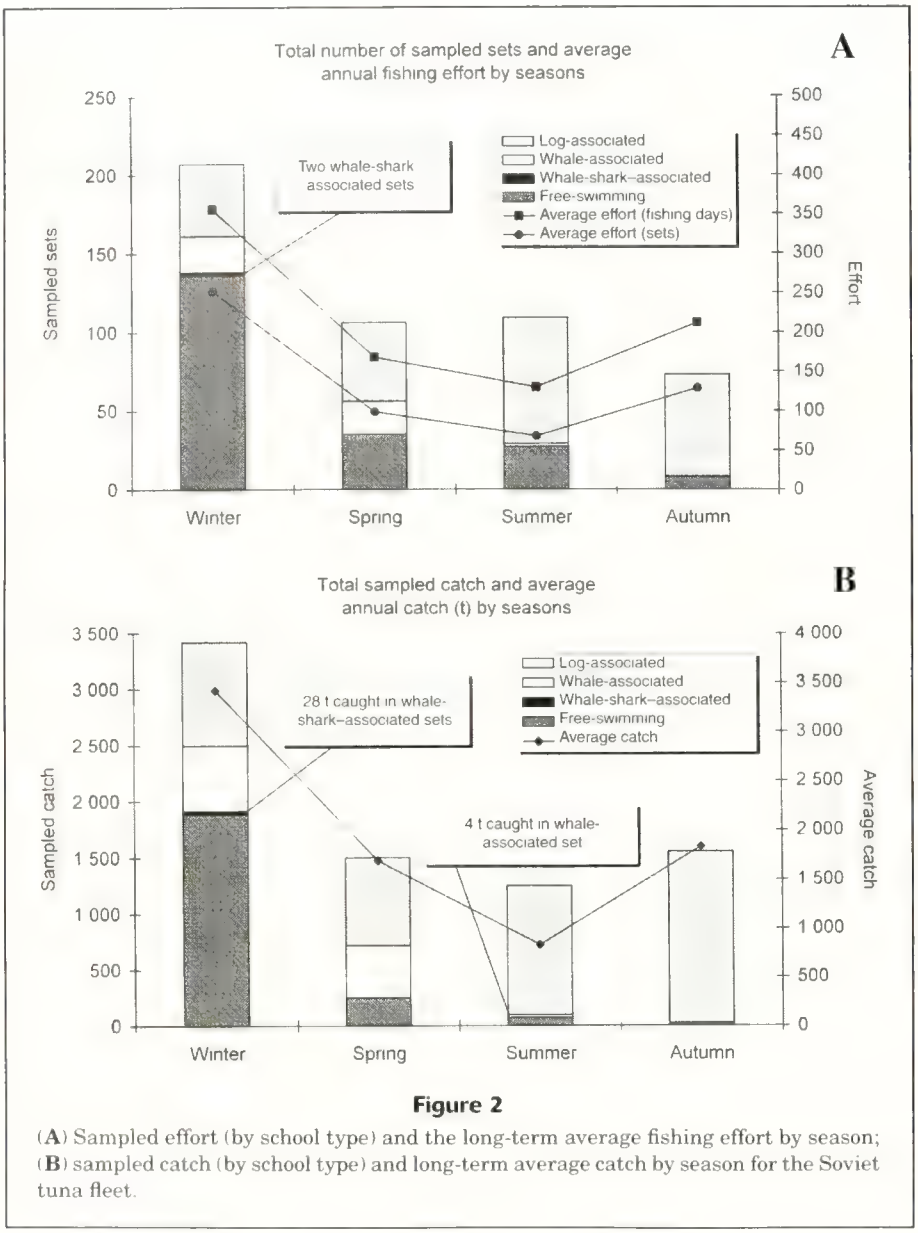

Figure 2

(**A**) Sampled effort (by school type) and the long-term average fishing effort by season; (**B**) sampled catch (by school type) and long-term average catch by season for the Soviet tuna fleet.

believe that the observers' data are representative of the catch by the Soviet purse-seine fleet in terms of sample size and geographical distribution of the sets.

The data series available for analysis was a combination of samples different in size, obtained in different years and seasons (Tables 1–3). Therefore the results of all analyses may have been subject to interannual variability (it is impossible to evaluate the effect of interannual variability from the data available), and the estimated average annual figures may have been subject to seasonal variability as well, on account of the unequal size of samples taken in different seasons.

Because the daily radio reports, which formed the basis of the database, did not include information on sets by school type, it was not possible to directly extrapolate the observers' data to the Soviet fleet separately by school types. However, I believe that the observers' data correctly reflect the seasonal ratio of sets on different school types.

To assess the possibility of using annual averages of the available samples and extrapolating them to the whole catch of the Soviet fleet, the author compared the seasonal magnitudes of total fishing effort (fishing days, sets) and catches reported by the Soviet fishing fleet (from the database) with the seasonal magnitudes of effort (number of sets) and catch (t) sampled by the observers (Fig. 2, A and B). The seasonal distribution of the sampled catch followed the same pattern as the long-term average seasonal distribution of the catch by the fleet (Fig. 2B). The effort did not fully agree with seasonal increase in the fishing effort of Soviet vessels during the autumn season (Fig. 2A), which may have resulted in a slight underestimation of average annual values of bycatch from log-associated

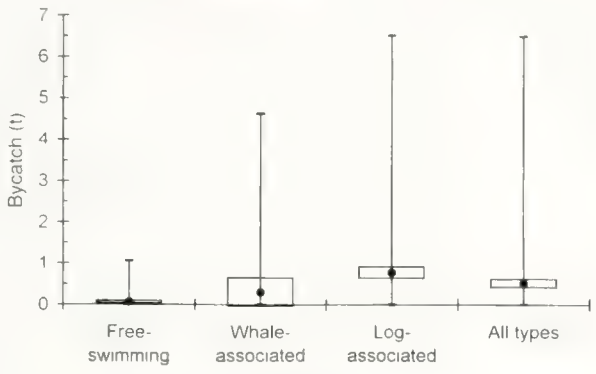

Figure 3

Bycatch per positive set in metric tons (t) by school type for the Soviet tuna purse-seine fishery. Dots are means, bars show range, and boxes are 95% confidence intervals.

schools. I did not attempt, however, to take this factor into consideration.

The average CPUE (e.g. total catch per set) in the purse-seine tuna fisheries varies greatly by type of vessel. I did not find a strong correlation between the bycatch per set and the total catch, or catch of target species in the same set. Level of bycatch generally depends on the type of association and the total fishing effort directed at this type of association.

Species composition and catch by school types

A total of 50 species (or higher taxa) of fishes and other marine animals were recorded in the catch of the fishing vessels (Table 4).

Free-swimming schools

Free-swimming schools are the predominant type of surface schools in the WIO. Such schools occurred in the area all year round (Table 2, Fig. 2, A and B). Soviet purse seiners set on free-swimming schools generally south of the equator (including Mozambique Channel)(Fig. 1B). Yellowfin, skipjack, and bigeye (*Thunnus obesus*) tunas were the principal components of free-swimming schools, comprising 80%, 15%, and 4%, respectively (Table 5). Monospecific (nonassociated) tuna schools, consisting completely of yellowfin or skipjack tuna, were found to occur in 47% of free-school sets. Multispecies free schools were observed in 53% of all free-school sets and generally consisted of two target species and bycatch. Bycatch occurred in 45% of the free-school sets, and nontuna bycatch in 22%.

A total of 19 species (or higher taxa of fishes) were observed in catches on free schools (Table 4). Some species were considered to be tuna prey (e.g. Exocoetidae) and some to be accidental bycatch (e.g. *Gempylus serpens, Canthidermis maculatus, Diodon* spp.). Nontuna bycatch in this type of association was on average 0.060 ±0.031 t per positive set (Fig. 3) and 3.403 ±2.770 t per 1000 t of target species (Fig. 4). The bulk of this bycatch was sharks of the genus *Carcharhinus* (0.023 t/1.296 t), rays of the Mobulidae family (0.020 t/1.128 t), marlins of the genus *Makaira*, and sailfish (*Istiophorus platypterus*) (0.016 t/0.895 t) (Tables 4 and 6). In the present study, bycatches are presented in parentheses as t per positive set/t per 1000 t of target species.

Whale-shark–associated schools

Two schools associated with whale sharks were sampled only in the winter season (Table 2, Fig. 2, A and B) south of the equator (Fig. 1C). In these sets, the bycatch consisted of the shark itself and a small quantity of albacore (*Thunnus alalunga*) (Table 4). This small sample size prohibited reliable bycatch estimates for whale-shark–associated schools and inferences of the species compositions of such associations.

Whale-associated schools

In the observers' logbooks, among the 45 sets on whale-associated tuna schools, 13 sets were made on schools associated with sei whales (*Balaenoptera borealis* Lesson, 1828) and one set on a school associated with a fin whale (*B. physalus* (Linnaeus, 1758)).[12] The remaining sets were made on unidentified baleen whales. According to verbal reports by some observers,[13] tuna schools associated with Bryde's whale (*B. edeni* Anderson, 1878), Minke whales (*B. acutorostrata* Lacépède, 1804), and pygmy blue whales (*B. musculus brevicauda* Linnaeus, 1758) were also observed in the WIO. From personal observations and those of the observers, sperm whales (*Physeter catodon* Linnaeus, 1758) were found often in the areas of the tuna purse-seine fishery; tunas, on the other hand, were not observed to associate with sperm whales. According to observations made during setting and searching operations, whales associated with tunas generally were found in groups of up to 8 individuals, more often in groups of 2–3 whales.

Whale-associated schools were most often observed from January to April. A whale-associated school was observed in July north of the equator (Table 2, Figs. 1C, 2, A and B). Schools of this type were distributed mainly south of the equator at latitudes 4–9°S. Skipjack, yellowfin, and bigeye tunas dominated in whale-associated schools—59%, 32%, and 6%, respectively (Table 5). The percentage of each species in different sets varied greatly: 0–100% for skipjack, 0–100% for yellowfin, and 0–74% for bigeye tuna. Associations consisting of one tuna species and a whale were encountered in eight cases (22%). Bycatch in whale-associated schools was found in 68% of the sets, and nontuna bycatch in 43% of the sets.

During sets on whale-associated schools, the fishermen keep the whale(s) inside the purse seine as long as pos-

[12] Species identification could be erroneous.

[13] Bashmakov, V. F. 1990. Personal commun. Atlantic Scientific Research Institute of Marine Fisheries and Oceanography (AtlantNIRO), 5 Dmitry Donskoy St., Kaliningrad, 236000, Russia.

Table 4

Species composition of tuna purse-seine catches in the western Indian Ocean. "?" denotes doubtful, in the author's opinion, species identification by observer.

	School type		
Family and species	Free-swimming	Whale-associated	Log-associated
Pisces			
Dasyatidae			
Dasyatis spp.	+		+
Mobulidae			
Manta birostris (Donndorff, 1798)	+?	+?	+
Mobula spp.	+	+	+
Rhincodontidae			
Rhincodon typus Smith, 1828[1]			
Lamnidae			
Isurus oxyrinchus Rafinesque, 1809		+	
Isurus spp.		[2]	
Carcharhinidae			
Carcharhinus falciformis (Bibron, 1839)	+	+	+
C. longimanus (Poey, 1861)	+	+	+
?C. obscurus (LeSueur, 1818)		+?	+[2]
Carcharhinus spp.		[2]	[2]
Sphyrnidae			
Sphyrna lewini (Griffith & Smith, 1834)			+
Sphyrna spp.			+
Exocoetidae sp.	+		
Belonidae sp.			+
Tylosurus crocodilus (Peron & LeSueur, 1821)			+
Lampidae			
Lampris guttatus (Brünnich, 1788)			+
Sphyraenidae			
Sphyraena barracuda (Walbaum, 1792)			+
Sphyraena spp.			+
Carangidae			
Caranx spp.			+
Decapterus macarellus Cuvier, 1833			+
Decapterus spp.			+
Elagatis bipinnulata (Quoy & Gaimard, 1824)	+		+
Seriola spp.	+		+
Naucrates ductor (Linnaeus, 1758)			+
Coryphaenidae			
Coryphaena hippurus Linnaeus, 1758		+	+
Coryphaena spp.			+
Kyphosidae			
Kyphosus cinerascens (Forsskål, 1775)			+
Gempylidae			
Gempylus serpens Cuvier, 1829	+		
Ruvettus pretiosus Cocco, 1829			+
Ephippididae			
Platax spp.		+	+
Scomberomoridae			
Scomberomorus commerson (Lacépède, 1800)			+
Scomberomorus spp.			+
Scombridae			
Acanthocybium solandri (Cuvier, 1831)			+

continued

Table 4 (continued)

Family and species	School type		
	Free-swimming	Whale-associated	Log-associated
Pisces (continued)			
Auxis rochei (Risso, 1810)			+
Auxis thazard (Lacepede, 1800)	+	+	+
Euthynnus affinis (Cantor, 1849)			+
Katsuwonus pelamis (Linnaeus, 1758)	+	+	+
Thunnus alalunga (Bonnaterre, 1788)	+		+
Thunnus albacares (Bonnaterre, 1788)	+	+	+
Thunnus obesus (Lowe, 1839)	+	+	+
Istiophoridae			
Istiophorus platypterus (Shaw & Nodder, 1792)	+		
Makaira indica (Cuvier, 1832)		+	+
M. mazara (Jordan et Snyder, 1901)	+		+
Makaira spp.	+		+
Tetrapturus audax (Philippi, 1887)			+
Xiphiidae			
Xiphias gladius (Linnaeus, 1758)			+
Nomeidae			
Cubiceps pauciradiatus Günter, 1872		+	
Balistidae			
Canthidermis maculatus (Bloch, 1786)	+		+
Monacanthidae			
Aluterus monoceros (Linnaeus, 1758)			+
Aluterus spp.			+
Diodontidae			
Diodon spp.	+		+?
Mammalia			
Balaenopteridae			
Balaenoptera borealis Lesson, 1828		+	
Salpae		+	
Ctenophora		+	
Chelonidea			+
Number of species (taxa)	19	17	45

[1] Recorded in whale-shark associated schools

Table 5

Average tuna catch per positive set (t) by "Rodina"-type Soviet vessels in the western Indian Ocean (total and by species). YFT = yellowfin tuna, SKJ = skipjack tuna, BET = bigeye tuna, ALB =albacore, FRI = frigate tuna, KAW = kawakawa. + = catch was <0.001 t.

Type of school	Total	Species					
		YFT	SKJ	BET	ALB	FRI	KAW
Free-swimming	18.4 ±5.2	14.7 ±4.9	2.8 ±1.7	0.8 ±1.0	0.03 ±0.03	0.05 ±0.06	—
Whale-associated	31.0 ±9.3	9.8 ±4.3	18.3 ±8.5	2.0 ±2.4	—	0.2 ±0.2	—
Log-associated	20.6 ±3.2	4.9 ±0.9	13.9 ±2.7	0.6 ±0.2	0.04 ±0.04	0.3 ±0.3	0.001 ±0.001
Total	20.6 ±2.7	8.6 ±1.8	10.5 ±1.9	0.8 ±0.4	0.03 ±0.03	0.2 ±0.2	+

Table 6

Estimates of the bycatch (t) of various species (groups) of marine animals by school type. The numerator is the average values per a positive set, the denominator is the average values per 1000 t of target species. + = catch was <0.001 t.

Species or group of species	School type[1]			
	Free-swimming	Whale-associated	Log-associated	All types of schools
Billfishes (Istiophoridae, Xiphiidae)	0.016/0.895	0.006/0.218	0.019/1.008	0.017/0.880
Wahoo (*A. solandri*)	—	—	0.031/1.621	0.018/0.934
Sharks (Lamnidae, Carcharhinidae, Sphyrnidae)	0.023/1.296	0.289/10.302	0.175/9.288	0.151/7.938
Rainbow runner (*E. bipinnulata*)	0.001/0.054	—	0.195/10.314	0.114/5.962
Dolphinfishes (*C. hippurus*)	+/0.027	0.001/0.051	0.191/10.098	0.111/5.836
Barracuda (*S. barracuda*)	—	—	0.002/0.132	0.001/0.076
Triggerfishes (*C. maculatus, Aluterus* spp.)	+/+	—	0.137/7.277	0.080/4.195
Mackerel scad (*D. macarellus*)	—	—	0.0093/0.491	0.005/0.283
Mantas, mobulas (Mobulidae)	0.020/1.128	0.009/0.318	0.002/0.126	0.009/0.455
Sea turtles	—	—	+/0.025	+/0.014
Other bycatch	+/0.002	+/0.003	0.018/0.958	0.011/0.553
Total For positive set	0.060 ±0.031	0.306 ±0.344	0.780 ±0.144	0.518 ±0.099
Total For 1000 t of target species	3.403 ±2.770	10.891 ±15.787	41.337 ±14.281	27.127 ±8.869

[1] Because of the small sample size, estimates of bycatch for whale-shark–associated schools are not presented in the Table.

Figure 4

Bycatch (t) per 1000 t of target species by school type for the Soviet tuna purse-seine fishery. Dots are means, bars are 95% confidence intervals.

sible. Whales often remain in the net until the end of pursing and then escape from the purse seine by either diving under the purse line, by ramming through the net wall, or by sinking the corkline (a rare occurrence).

Observers registered a single case of entanglement in the net and subsequent death of a young sei whale about 10 m in length and about 12 t in weight. The dead animal was taken up on the vessel's deck, released from the purse seine, and discarded into the ocean. It is not possible to assess the frequency and probability of whale mortality by the purse-seine fishery in the WIO.

There were 17 species (or groups) of marine animals identified in the catches of whale-associated schools (Table 4). Salps, ctenophores, and batfish (*Platax* spp.) were considered accidental bycatch, whereas long-finned fathead (*Cubiceps pauciradiatus*) was a prey item of both tunas and whales. Nontuna bycatch in this type of association averaged 0.306 ±0.344 t for a positive set or 10.891 ±15.787 t per 1000 t of target species (Figs. 3 and 4). Sharks of the genus *Carcharhinus* and *Isurus* made up the bulk of the bycatch in whale-associated school sets (0.289 t/10.302 t) (Tables 4 and 6).

Log-associated schools

Log-associated schools are one of the predominant school types found in the WIO all year round (Table 2, Fig. 2, A and B). Sets on log-associated schools were made throughout the sampling area as far south as 15°S (Fig. 1D). In log-associated schools the bulk of the catch were skipjack, yellowfin, and bigeye tunas—67%, 24%, and 3%, respectively (Table 5). Log-associated schools in all cases consisted of several fish species. Bycatch was found in 93% of the sets, and nontuna bycatch in 87%. The absence of bycatch was rare, observed only during successive sets on the same floating object.

The species composition associated with floating objects was the most diverse of any set type and included 45 species (or higher taxa of fishes) (Table 4). Nontuna bycatch was at its highest in log-associated sets, as much as 0.780 ±0.144 t per positive set or 41.337 ±14.281 t per 1000 t of target species (Figs. 3 and 4). The bulk of the bycatch in sets on log-associated schools was made up of rainbow runner,

Elagatis bipinnulata (0.195 t/10.314 t), common dolphinfish, *Coryphaena hippurus* (0.191 t/10.098 t), triggerfish of the genus *Canthidermis* (0.137 t/7.277 t), sharks of the genus *Carcharhinus* (0.175 t/9.288 t), wahoo, *Acanthocybium solandri* (0.031 t/1.621 t), billfishes of the genera *Makaira* and *Tetrapturus* (0.019 t/1.008 t), and mackerel scad, *Decapterus macarellus* (0.0093 t/0.491 kg). One capture of a sea turtle (unknown species) was recorded (Tables 4 and 6).

All types of schools

Considering all school types in the aggregate, skipjack, yellowfin, and bigeye tuna prevailed in the catch —51%, 42%, and 4% by weight, respectively (Table 5). Albacore represented a mere 0.2%, frigate tuna 0.9%, and kawakawa, *Euthynnus affinis*, less than 0.1%. Nontuna bycatch accounted for less than 3% of the catch.

On the average, there was 0.518 ±0.099 t of nontuna bycatch caught per positive set, or 27.127 ±8.869 t per 1000 t of target species (Fig. 3). Bycatch levels by species (groups) are given in Table 6.

Discussion

The lowest fish bycatch in the WIO tuna purse-seine fishery was taken from free schools (mainly carcharhinid sharks and Mobulidae rays) (Figs. 3 and 4, Tables 4 and 6). Bycatch of fishes was highest and most diverse from catches on log-associated schools. Rainbow runner, common dolphinfish, triggerfish, carcharhinid sharks, wahoo, billfishes, and mackerel scad were predominant. Whale-associated schools were characterized by an intermediate level of bycatch (mainly carcharhinid and lamnid sharks) (Figs. 3 and 4, Tables 4 and 6).

It is interesting to compare the bycatch rates obtained in this study with those published for other regions. The principal bycatch fishes in the Pacific (Bailey et al., 1996; Hall, 1996, 1998; Anonymous, 1997) are the same as those presented here. Bycatch levels are known to vary considerably by year, area, fleet (Bailey et al., 1996; Hall, 1996; Anon., 1997), and school type; this variability hampered direct comparisons of the results from the present study with those from published data. However, for the purpose of comparison, I pooled my estimates by groups in accordance with the published data (Bailey et al., 1996; Hall, 1996, 1998; Anonymous, 1997). Bycatch levels per set and per 1000 t of target species for various regions of the Pacific and my estimates for the Indian Ocean are on the same order of magnitude for most groups in similar types of associations (Figs. 5 and 6).

I also attempted to estimate the unrecorded bycatch by the purse-seine fleets of the principal fishing nations of the WIO by a comparison of fishing tactics. The Soviet fleet in the WIO made an equal proportion of sets on free-swimming schools and on log-associated schools during the year (Table 2). Seasonally they switched effort from sets on free-swimming schools to those on log-associated schools (Fig. 7, A and B). The fishing practices of French and Spanish tuna seiners showed similar seasonality until the mid-1990s (Anonymous;[14,15,16] Pianet;[17,18] Moron[19]).

The fishing tactics of the Japanese (Hallier;[20] Okamoto and Miyabe[21]) and Mauritian (Norungee et al.;[22] Norungee and Lim Shung[23]) purse-seine fleets differed considerably from that described above. Japanese and Mauritian vessels made sets on log-associated schools all year round, with single instances of sets on other schools types.

Only two school types (log schools and free schools) have been described by Hallier;[20] Hallier;[24] Parajua Aranda;[25]

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continued

Table 7

Bycatch estimates in tons in the western Indian Ocean purse-seine fisheries during 1985–94. MIX = fleets targeted all types of schools (France, Spain, USSR), LOG = fleets targeted log-associated schools (Japan and Mauritius).

Species, a group of species		1985	1986	1987	1988	1989	1990	1991	1992	1993	1994
	MIX	913	1047	1257	1674	1622	1503	1471	1793	1796	1925
Pelagic oceanic sharks	LOG	31	30	61	81	108	180	278	477	451	143
	Total	944	1077	1318	1755	1730	1683	1749	2270	2247	2068
	MIX	686	786	944	1257	1218	1129	1105	1347	1349	1446
Rainbow runners	LOG	34	33	68	90	120	199	309	530	500	159
	Total	720	819	1012	1347	1338	1328	1414	1877	1849	1605
	MIX	671	770	925	1231	1193	1105	1082	1318	1320	1415
Dolphinfishes	LOG	34	33	67	88	117	195	303	518	490	156
	Total	705	803	992	1319	1310	1300	1385	1836	1810	1571
	MIX	483	554	665	885	857	794	778	948	949	1017
Triggerfishes	LOG	24	24	48	64	84	141	218	374	353	113
	Total	507	578	713	949	941	935	996	1322	1302	1130
	MIX	108	123	148	197	191	177	173	211	211	227
Wahoo	LOG	5	5	11	14	19	31	49	83	79	25
	Total	113	128	159	211	210	208	222	294	290	252
	MIX	101	116	139	185	180	167	163	199	199	213
Billfishes	LOG	3	3	7	9	12	20	30	52	49	16
	Total	104	119	146	194	192	187	193	251	248	229
	MIX	52	60	72	96	93	86	84	103	103	110
Mobulas and mantas	LOG	<1	<1	1	1	1	2	4	6	6	2
	Total	53	60	73	97	94	88	88	109	109	112
	MIX	33	37	45	60	58	54	53	64	64	69
Mackerel scad	LOG	2	2	3	4	6	10	15	25	24	8
	Total	35	39	48	64	64	64	68	89	88	77
	MIX	9	10	12	16	16	14	14	17	17	19
Barracudas	LOG	<1	<1	1	1	1	3	4	7	6	2
	Total	9	11	13	17	17	17	18	24	23	21
	MIX	64	73	88	117	113	105	102	125	125	134
Other fishes	LOG	3	3	6	8	11	18	29	49	47	15
	Total	67	76	94	125	124	123	131	174	172	149
	MIX	3120	3576	4295	5718	5541	5134	5025	6125	6135	6574
Total nontuna bycatch	LOG	137	134	273	360	479	799	1239	2121	2004	638
	Total	3257	3710	4568	6078	6020	5933	6264	8246	8139	7212

Anonymous;[14, 15, 16] Pianet;[17, 18] Hastings and Domingue;[26] and Moron[19] for the tuna purse-seine fishery in the Indian Ocean. Free schools in these analyses included all types of associations with marine animals. The proportion of sets of the French fleet on other types of schools and on resulting catches is not known. Cort (1992) presented such data for Spanish vessels, based on fishing logbooks. Therefore, I used the observers data of the Seychelles Fishing Authority (SFA) (Cort, 1992) for the vessels of France, Spain, Japan, and USSR to assess these values in the WIO. The percentage of sets on whale-associated schools varied from 1.7% to 8.8% in 1986–90, the percentage among positive sets was from 1.2% to 9.1%, and the catch from such schools was 1.6% to 7.8% (cited from Cort, 1992). These values are slightly lower than the observer data I report in the present study (9%, 10%, and

[24] (continued) Proceedings of the expert consultation on Indian Ocean tunas, 5th session, Mahe, Seichelles, 4–8 October, 1993 (J. D. Ardill, ed.), p. 192–198. IPTP Coll. Vol. 8., TWS/93/2/25. FAO, Viale delle Terme di Caracalla, 00100, Rome, Italy.

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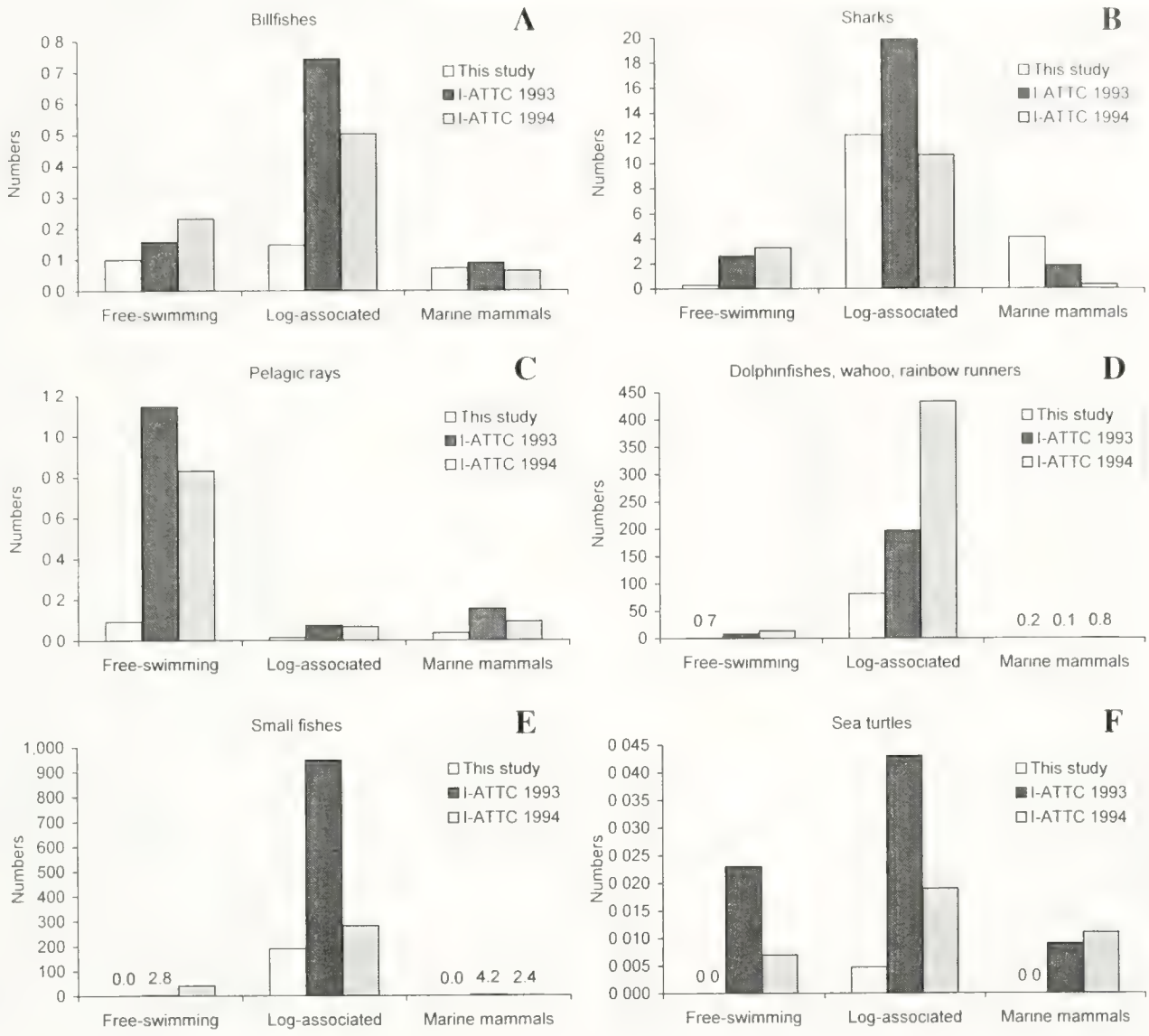

Figure 5

Bycatch levels in numbers per set by groups of species and by types of schools in the western Indian Ocean and eastern Tropical Pacific (Anonymous, 1997).

14%, respectively), which is explained by the fact that the SFA data included Japanese vessels known to fish on log-associated schools only. Nevertheless, the SFA values and those from our observers were on the same order of magnitude. Proceeding from this, I estimated the ratio of sets on various school types and the magnitude and species composition of bycatch by the French and Spanish vessels. These values were close to those for the Soviet fleet employing similar fishing tactics.[27]

Thus, the average bycatch estimates presented in this study can be extrapolated for this period to the total WIO purse-seine catch of principal fishing nations targeting all types of schools.[28] Estimates of bycatch from log-associated schools, I believe, can be extended, with some caution, to the pooled purse-seine catch of Japan and Mauritius in the WIO.

The annual purse-seine catches of yellowfin and skipjack tunas by fleets targeting all types of schools (France,

[27] Data from logbooks (Cort, 1992) show a lower proportion of sets and of catches on whale-associated schools for Spanish vessels, but in the author's view a comparison of data collected in the same way (by observers) is preferable.

[28] France and Spain (along with catch from the vessels from these two countries flying "flags of convenience" [Panama, Côte d'Ivoire, and recently Belize] and applying the same fishing tactics), and USSR (recently Russia or Liberia).

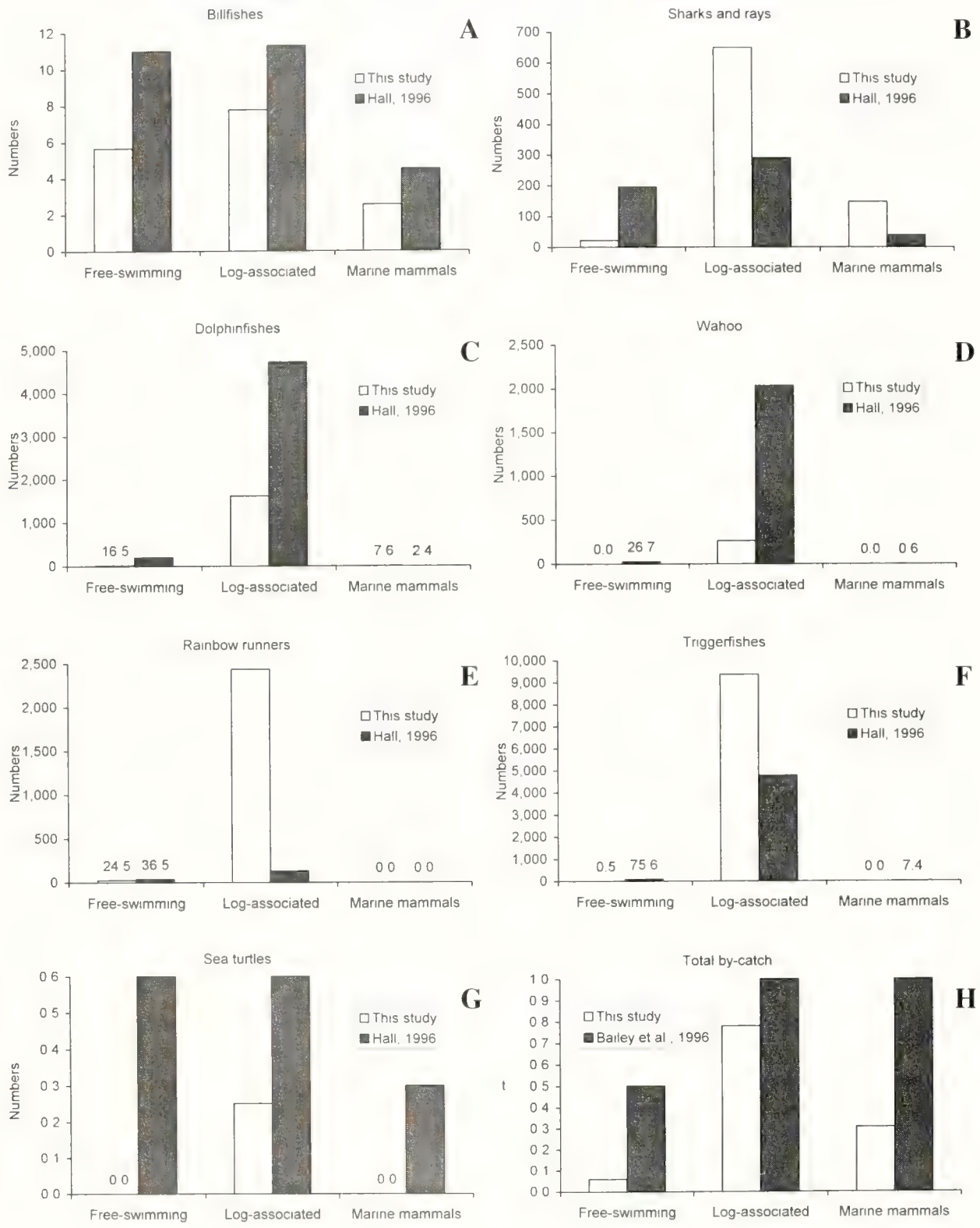

Figure 6

(**A–G**). Bycatch levels, in numbers per 1000 t of target species, by groups of species and by types of schools in the western Indian Ocean and eastern Tropical Pacific; (**H**) bycatch levels, in tons per set by types of schools in the western Indian Ocean and western Pacific Ocean.

Spain, and USSR)[29] in the WIO ranged between 115,000 and 242,000 t in 1985–94 (Anonymous[30]). Japanese and Mauritian catches varied from 3000 to about 51,000 t. Based on these values, the estimated bycatch was 3257 to 8246 t of various fishes during the same period (Table 7). These fishes could serve as food for the coastal countries of the area. Estimated bycatch in numbers is presented in Table 8.

Turtle bycatch and whale mortality in purse seines are also possible in the WIO, but the probability of the latter is very low. No instances of whale mortality have been recorded earlier for tuna purse-seine fisheries in other areas (Northridge, 1984, 1991a, 1991b; Medina-Gaertner and Gaertner, 1991; Santana et al., 1991; Cort, 1992; Cayre et al., 1993; Bailey et al., 1996). No avian mortality by the Soviet tuna purse-seine fishery has been noted by observers. A similar fact was reported for the western Pacific (Bailey et al., 1996).

Target fishing for rainbow runner, dolphinfish, triggerfishes, wahoo, mackerel scad, and barracuda is not conducted in the WIO, and these fish are taken only as bycatch. Their bycatch levels, estimated in this study, do not seem to endanger the populations of these species.

Estimated bycatch of billfishes (104–251 t annually) was less than 1% of the total catch for these species (14,000–33,000 t during 1985–94) in the WIO (Anonymous[30]). The bycatch by the purse-seine fishery was unlikely to substantially affect the billfish stocks.

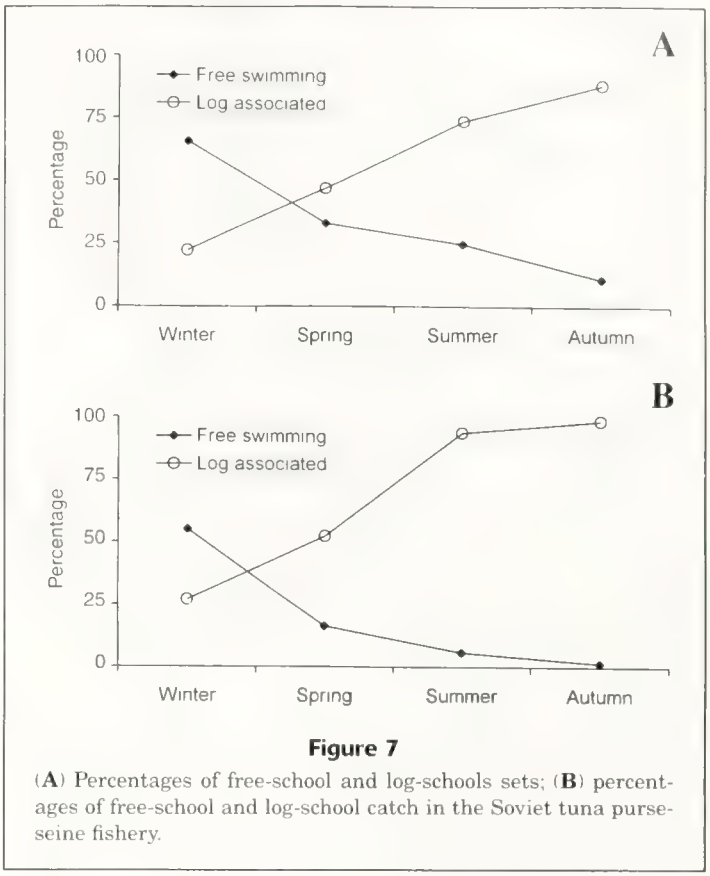

Figure 7

(**A**) Percentages of free-school and log-schools sets; (**B**) percentages of free-school and log-school catch in the Soviet tuna purse-seine fishery.

Many pelagic sharks are taken as bycatch by the longline, trawl, coastal driftnet, and other fisheries, but are not recorded. The total shark catch by all fisheries may be considerable. Many shark species are characterized by low abundance, low fecundity, long life span, and consequently, by high vulnerability to overfishing. Underestimation of the removal through fisheries of a number of pelagic shark species, and the impact of the fisheries on their populations, may lead to a reduction in their abundance to critical levels, diminishing the biodiversity of the pelagic ecosystem of the Indian Ocean.

Some part of the bycatch is released into the ocean alive, although subsequent survival rates are unknown. The lack of bycatch and discard records and estimates of survival rates of discarded animals prevents assessment of the impact of the fishery on the Indian Ocean pelagic ecosystem.

Fishing tactics in the WIO have changed considerably by all principal purse seine fleets toward the extensive use of FADs in recent years (generally from 1995). The majority of Japanese vessels have left the area and have moved to the eastern Indian Ocean. Therefore estimates presented here for total WIO purse-seine fisheries are applicable for a limited time span only (pre-1995). Recent development of the WIO fisheries warrants further investigation of bycatches through extensive observer sampling by time–area strata.

Establishing a scientific program by the Indian Ocean Tuna Commission to monitor the principal tuna fisheries in the region, by placing international scientific observers on purse-seine and longline vessels, might be the first step toward a more accurate assessment of the impact of bycatches on the epipelagic ecosystem of the Indian Ocean. This program might also lead to developing technical and management measures to reduce the bycatches or to use them.

The solution to the bycatch problem should take two directions: 1) an effort to reduce or eliminate bycatches of undesired species; or 2) to use bycatch animals to make them target species. The former involves developing gear modifications or changes in fishing tactics. The latter involves management regulation of the fishery so that bycatch species are treated in the same way as other target species.

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[29] Including vessels flying flags of convenience.

[30] Anonymous. 1998. Indian Ocean tuna fisheries data summary, 1986–1996. Indian Ocean Tuna Commission (IOTC) data summary 18, 180 p. IOTC, P.O. Box 1011, Victoria, Seychelles.

Table 8

Bycatch estimates in numbers in the western Indian Ocean purse-seine fisheries during 1985–94. Codes are same as table 7. MIX = fleets targeted all types of schools (France, Spain, USSR); LOG = fleets targeted log-associated schools (Japan and Mauritius).

Species, a group of species		1985	1986	1987	1988	1989	1990	1991	1992	1993	1994
Pelagic oceanic sharks	MIX	45,600	52,273	62,780	83,581	80,993	75,052	73,455	89,529	89,676	96,094
	LOG	2161	2100	4280	5653	7531	12,546	19,456	33,320	31,488	10,030
	Total	47,761	54,373	67,060	89,234	88,524	87,598	92,911	122,849	121,164	106,124
Rainbow runners	MIX	162,457	186,232	223,664	297,770	288,550	267,386	261,694	318,961	319,485	342,351
	LOG	8112	7883	16,065	21,218	28,267	47,090	73,029	125,065	118,190	37,646
	Total	170,569	194,115	239,729	318,988	316,817	314,476	334,723	444,026	437,675	379,997
Dolphinfishes	MIX	107,711	123,473	148,291	197,424	191,312	177,280	173,505	211,474	211,821	226,982
	LOG	5373	5221	10,641	14,053	18,723	31,190	48,370	82,835	78,282	24,934
	Total	113,084	128,694	158,932	211,477	210,035	208,470	221,875	294,309	290,103	251,916
Triggerfishes	MIX	621,823	712,823	856,096	1,139,747	1,104,458	1,023,450	1,001,661	1,220,857	1,222,862	1,310,387
	LOG	31,215	30,334	61,820	81,646	108,774	181,205	281,018	481,252	454,799	144,863
	Total	653,038	743,156	917,916	1,221,393	1,213,232	1,204,655	1,282,679	1,702,109	1,677,661	1,455,250
Wahoo	MIX	17,444	19,996	24,016	31,973	30,983	28,710	28,099	34,248	34,304	36,760
	LOG	876	851	1734	2290	3051	5083	7883	13,501	12,759	4064
	Total	18,320	20,847	25,750	34,263	34,034	33,793	35,982	47,749	47,063	40,824
Billfishes	MIX	750	859	1032	1374	1332	1234	1208	1472	1474	1580
	LOG	26	25	51	68	90	151	233	400	378	120
	Total	776	884	1083	1442	1422	1385	1441	1872	1852	1700
Mobulas and mantas	MIX	250	286	344	458	444	411	403	491	491	527
	LOG	3	2	5	7	9	15	23	39	37	12
	Total	253	288	349	465	453	426	426	530	528	539
Mackerel scad	MIX	45,134	51,739	62,138	82,726	80,164	74,285	72,703	88,613	88,758	95,111
	LOG	2266	2202	4487	5926	7895	13,153	20,398	34,931	33,011	10,515
	Total	47,340	53,941	66,625	88,652	88,059	87,438	93,101	123,544	121,769	105,626
Barracudas	MIX	1350	1547	1858	2474	2397	2221	2174	2650	2654	2844
	LOG	68	66	134	177	236	393	610	1044	987	314
	Total	1418	1613	1992	2651	2633	2614	2784	3694	3641	3158

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Ontogenetic shifts in natural diet during benthic stages of American lobster (*Homarus americanus*), off the Magdalen Islands

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Abstract—The natural diet of 506 American lobsters (*Homarus americanus*) ranging from instar V (4 mm cephalothorax length, CL) to the adult stage (112 mm CL) was determined by stomach content analysis for a site in the Magdalen Islands, Gulf of St. Lawrence, eastern Canada. Cluster and factor analyses determined four size groupings of lobsters based on their diet: <7.5 mm, 7.5 to <22.5 mm, 22.5 to <62.5 mm, and ≥62.5 mm CL. The ontogenetic shift in diet with increasing size of lobsters was especially apparent for the three dominant food items: the contribution of bivalves and animal tissue (flesh) to volume of stomach contents decreased from the smallest lobsters (28% and 39%, respectively) to the largest lobsters (2% and 11%, respectively), whereas the reverse trend was seen for rock crab *Cancer irroratus* (7% in smallest lobsters to 53% in largest lobsters). Large lobsters also ate larger rock crabs than did small lobsters. This study is the first to examine the natural diet of shelter-restricted juveniles (SRJs, <14.5 mm CL), which were thought to be principally suspension feeders and to a lesser degree browsers or ambush predators in or near their shelter. However, at our study site no planktonic organisms were identified from the stomachs of SRJs, whereas formaniferans, crustacean meiofauna, and macroalgal debris that could be derived by browsing, together represented only 10–14% by volume of stomach contents. We infer that SRJs obtained bivalves by predation and flesh by exploiting larger lobsters' meal scraps or food reserves. Some implications of these findings for lobster artificial reef programs and for the conservation of lobster stocks are discussed.

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American lobster, *Homarus americanus*, is a long-lived, dominant predator in temperate coastal waters of eastern North America (Elner and Campbell, 1991; Ojeda and Dearborn, 1991). After the larval phase, lobsters settle and spend much of their time in burrows or natural shelters (Cobb, 1971; Lawton, 1987; Barshaw and Bryant-Rich, 1988). However, laboratory and *in situ* observations indicate that benthic lobsters pass through successive life-history phases as they grow in size, changing from a shelter-restricted habit to a more overt lifestyle involving daily forays and seasonal migrations away from shelter (Cooper and Uzmann, 1977; Cobb and Wahle, 1994). A variety of classifications have been proposed for these successive ontogenetic phases. The latest scheme, by Lawton and Lavalli (1995), recognizes five life-history phases: shelter-restricted juvenile (SRJ, ~4–14 mm cephalothorax length, CL), emergent juvenile (~15–25 mm CL), vagile juvenile (~25 mm CL to size of physiological maturity), adolescent, and adult.

In several decapod crustaceans, diet changes as individuals grow and become more mobile and their chela size and strength increases (e.g. Lee and Seed, 1992; Freire et al., 1996). Such dietary shifts should occur in the lobster as well, especially considering this species' changing dependency on shelter which, in turn, has implications for foraging range and accessibility of prey types (Elner and Campbell, 1987; Lawton, 1987). Some studies of the natural diet of lobsters 12–125 mm CL have found little or no differences in the identity or in the frequency of food items that were ingested by different size groups (Weiss, 1970; Ennis, 1973; Hudon and Lamarche, 1987). However, other studies have pointed to changes in the identity and especially in the frequency of food items ingested by different lobster size groups. Carter and Steele (1982b), using their own results and data from nonconcomitant studies conducted at different sites in Newfoundland (Squires, 1970; Ennis, 1973), have suggested that lobsters of 12–73 mm CL consume sea urchins, ophiuroids, and mussels more frequently than larger (adult) lobsters. Scarratt (1980) reported that lobsters consumed more crabs, mussels, and fish, but fewer echinoderms, as they grew in size and approached maturity. This trend was attributed to differential accessibility of prey. Elner and Campbell (1987) indicated that the stronger chelae of larger lobsters would enable them to crush prey that are protected by heavy shells, such as gastropods and bivalves, more so than the chelae of smaller lobsters.

The natural diet of SRJ lobsters has not been examined to date (Lawton and Lavalli, 1995), excepting rare specimens of 12–14 mm CL. The feeding appendages of SRJs are capable of capturing and processing both planktonic and benthic organisms (Lavalli and Factor, 1995). From laboratory observations, several authors have proposed that SRJs may live primarily as suspension-feeders, and to a lesser degree as browsers, within the shelter or as ambush predators at the shelter's entrance (Barshaw and Bryant-Rich,

1988; Barshaw, 1989; Lavalli and Barshaw, 1989; Lawton and Lavalli, 1995). Wahle (1992) offered a conceptual model suggesting that lobsters shift from a cryptic to a wide-roaming behavior as predation risk becomes offset by the need for a high-energy diet that cannot be satisfied through shelter-restricted feeding.

Our study was conducted at the Magdalen Islands, eastern Canada, to resolve the natural diet of SRJ lobsters and to compare it with that of larger lobsters by using stomach content analysis. We found a gradual ontogenetic shift in lobster diet over the size range of 4 to 112 mm CL. SRJs were carnivorous and probably derived their meals mainly through predation and scavenging. We also determined the predator-prey size relationship for one of the lobster's preferred and most important prey, i.e. Atlantic rock crab, *Cancer irroratus* (Reddin, 1973; Evans and Mann, 1977; Carter and Steele, 1982a).

Materials and methods

The study site was a narrow 2-km rocky section (47°14.5′N, 61°50.5′ to 61°51.3′W) of the south shore of Baie de Plaisance, Magdalen Islands, eastern Canada. This site corresponds to the Butte-à-la-Croix location that Hudon (1987) determined to be a settlement ground for lobster. Divers collected lobsters by hand or by suction-sampling at depths of 1 to 7 m. Lobsters were processed live usually within minutes and at most two hours after collection. The sex of collected specimens was determined and their CL was measured to the nearest 0.1 mm with a vernier caliper. Lobsters that were not berried and that were judged to be intermolt, based on criteria of shell hardness, coloration, and fouling in Aiken (1980), were dissected to remove the stomach which was preserved in buffered formalin diluted to 4% in seawater. Stomachs with calcified gastroliths were subsequently disregarded, thereby effectively eliminating from the present study all premolt lobsters from stage $D^{1.5}$ ($=D_0$) on (Aiken, 1980). The resulting sample consisted of 471 stomachs from lobsters of 7–112 mm cephalothorax length (CL) collected from 24 July to 31 October 1996, and of 35 stomachs from lobsters of 4–12 mm CL collected between 4 August and 13 September 1997. The 1997 lobsters were added to improve coverage of stomach contents of the early juveniles because very little settlement occurred in 1996 (Sainte-Marie et al., 2001). There was no commercial fishery during the sampling periods; therefore items in lobster stomachs were not discards or bait.

In the laboratory, stomachs were opened and their content was emptied into dishes for examination under a Wild M8 compound microscope (10–50×). Identity of food items was determined to the lowest taxonomic level possible, based on comparisons with illustrations in literature and samples of benthic and pelagic fauna from our study site. Particular care was taken when examining the stomach contents of lobsters <12 mm CL; for these stomach contents we often resorted to higher magnification (>100×) with a Leitz Dialux 20 microscope.

The contribution of each food item, exclusive of minerals and nylon debris, to the volume of stomach contents of each lobster was visually scored from 0 to 10, by 10% increments (0=0% of volume, 1=1–10%, 2=11–20%, etc.). The total for all food items could exceed 10, for example, if more than two minor food items each were scored 1 in addition to one predominant food item that was scored 8. In such cases, the corrected contribution of each food item was obtained by dividing its score by the sum of scores for all organic food items in a given stomach. Corrected volumetric contribution of each food item was expressed as a proportion of stomach content volume.

To obtain information on the size spectrum of rock crab consumed by lobsters, we established predictive (least squares) linear regressions (Sokal and Rohlf, 1995) between 30 measurements of distinctive hard body parts and cephalothorax width (CW) of 26 crabs ranging from 7 to 62 mm CW (following the approach in Lovrich and Sainte-Marie, 1997). All the predictive regressions were highly significant (r^2=0.970–0.999, P<0.001). When rock crab remains were encountered in lobster stomachs, distinctive hard body parts were measured with an eyepiece micrometer to estimate crab CW from predictive regressions. When more than one body part could be measured, the crab's CW was determined as the mean of the various estimates unless it was obvious that multiple crabs had been ingested. Such was considered to be the case when more than two similar fragments of a paired structure (e.g. eyes or claws) were found in one lobster stomach or when there was considerable divergence among crab CW estimates based on different body parts. The functional relationship between the CW of rock crab prey and the CL of lobster predators was established with a model II regression (Laws and Archie, 1981; Sokal and Rohlf, 1995).

The stomach contents, once identified and scored for volume, were transferred separately to preweighed trays, dried to constant mass at 60°C, and weighed to the nearest mg. Dry mass was not obtained for eight stomach contents because of manipulation errors. The allometric relationship between the dry mass of stomach contents and lobster CL was established by least squares linear regression, after logarithmic transformation of both variables.

Diet was described by occurrence, volumetric contribution, and the specific abundance of food items in the stomachs of lobsters grouped into 5-mm CL size classes (2.5 to <7.5 mm, 7.5 to <12.5 mm, etc.). Percent occurrence (PO) was the percentage of stomachs in one size class that contained a given food item. Volumetric contribution (VC) was the average of corrected contributions of each food item to the stomachs of all lobsters in a given size class. Specific abundance (SA) was the average volumetric contribution of a food item determined only for lobsters that had this food item in their stomach. This index is useful for food items with a low average volumetric contribution because it allows the distinction between the case when few animals consume large quantities of a given food item or when many animals consume small quantities of the same food item (Amundsen et al., 1996). The mathematical relationship of the three indices is $SA = VC \times 100/PO$.

To assess how the overall diet varied with lobster size, and thus whether or not there were size-related shifts in diet supporting the ontogenetic phases of lobster, we

performed a cluster analysis (Ward's minimum variance method) on the volumetric contribution of food items per lobster size class, after standardization. A sudden increase in the joining distance of the clustering sequence represented by the dendrogram represents a natural cutting point for the determination of meaningful clusters (SAS Institute, 1995). In addition, a factor analysis (VARIMAX rotation of the first three principal components) was performed on the correlation matrix of the volumetric contribution of food items for each 5-mm-CL size class of lobsters. Cluster and factor analyses were done with JMP statistical software (SAS Institute, 1995).

Relationships between volumetric contribution and lobster CL were described by least squares linear regression for bivalves, rock crab, and flesh. Relationships between percent occurrence of bivalves and rock crab were described by locally weighted (lowess) regression with a 60% smoothing factor, and by least-squares regression for flesh.

Results

Sample composition, stomach fullness, and types of food items

The 506 lobsters retained for analyses varied in size from 4.3 to 112.4 mm CL (median=35.6 mm CL). Most size classes contained more than 25 lobsters (Table 1). The smallest size class (2.5 to <7.5 mm CL) contained only 16 lobsters with a median of 7.0 mm CL; therefore we refer to this group of lobsters as the 7-mm-CL size class. The 21 lobsters ≥67.5 mm CL were pooled together into a single size class, which we refer to as the 77-mm-CL size class in reflection of their median CL. Females and males accounted respectively for 43.2% and 44.1% of all lobsters examined; the remainder were too small to determine sex. Lobsters were pooled for analyses irrespective of sex because Weiss (1970) and Ennis (1973) concluded that diet was the same for both sexes.

Only two lobsters had empty stomachs and they belonged to the 10-mm size class. With these two empty stomachs excluded, there was a highly significant relationship between the dry mass of stomach contents and lobster CL (Fig. 1). Identifiable food items included macroalgae or benthos that were grouped into broad taxonomic or ecological categories (Table 2). No planktonic organisms were identified from the stomachs, even of the smallest lobsters. However, the crustacean meiofauna group included the remains of very small crustaceans, some like the harpacticoids and ostracods, known to be bottom-dwelling, whereas unidentified minute crustacean remains may have originated from holo- or mero-planktonic forms or from juvenile amphipods, isopods, or carideans. Sand, silt, and infrequently bits of nylon rope were also found in the stomachs. "Flesh" refers to tissue bolus composed of animal soft parts that could not be attributed to a taxon, generally because no distinctive part was found in the stomach along with the tissue or less commonly because distinctive parts from several prey types were present in the stomach but none was attached to the tissue.

Table 1

Number of lobster stomachs sampled by classes of cephalothorax length (CL, in mm). Size classes represent 5-mm groupings except the smallest (7 mm CL) and largest (77 mm CL), which include all lobsters <7.5 mm CL and all lobsters ≥67.5 mm CL, respectively.

Cephalothorax length (size classes)	Number of stomachs		
	1996	1997	Total
7	1	15	16
10	17	20	37
15	28		28
20	38		38
25	56		56
30	45		45
35	52		52
40	51		51
45	45		45
50	45		45
55	31		31
60	25		25
65	16		16
77	21		21
Total	471	35	506

Ontogenetic shifts in diet

A cluster analysis on the volumetric contribution of food items to lobsters by size class yielded four groups: 7 mm, 10–20 mm, 25–60 mm, and 65–77 mm CL lobsters (Fig. 2). These same groups could be seen on a plot of the first three factors of a factor analysis of the correlation matrix of the volumetric contribution of food items (Fig. 3). The three factors explained 68.8% of the variance (39.9%, 18.2%, and 10.7% for factors 1, 2, and 3). The first factor had strong loadings for crustacean meiofauna (0.96), foraminiferans (0.96), bivalves (0.84), macroalgae (0.82), amphipods (0.78), and rock crab (–0.71). Because lobsters in the 7-mm-CL size class had little rock crab in their stomachs, but relatively high proportions of the other food items, they stood out with a very large score (3.1) on this factor. The next two size classes, 10 and 15 mm CL, scored 0.8 and 0.6, respectively. All other size classes scored between 0 and –0.6 on the first factor. The second factor had strong loadings for flesh (0.73), lobster (–0.82), and barnacles (–0.73). Lobsters of the two largest size classes (65 and 77 mm CL) had strong negative scores on this factor (–2.5 and –1.5, respectively), whereas lobsters of the 10–35 mm size classes scored between 0.5 and 1.1. The smallest size class (7 mm CL) and size classes of 40–60 mm CL had scores close to 0. Finally, the third factor had a high loading for carideans (0.74) and somewhat smaller loadings for isopods (0.67), coralline algae (–0.57), and pagurids (–0.54). This third factor separated

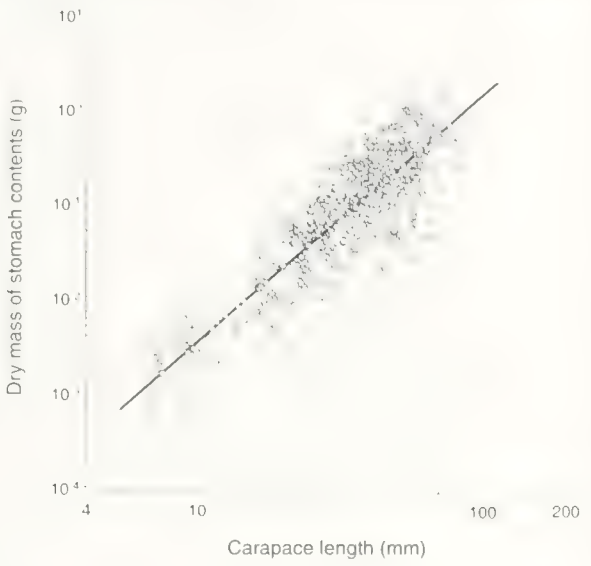

Figure 1

Relationship of dry mass of stomach contents (DM) to cephalothorax length (CL) of lobsters from the Magdalen Islands. Two lobsters of the 10-mm class had an empty stomach and are not shown. Model II regression: $DM = 7.967 \cdot 10^{-6} \cdot CL^{2.925}$ (r^2=0.51, P<0.001).

the 25- and 35-mm-CL size classes from the 10–20 mm CL size classes.

For each grouping, Figure 4 shows the specific abundance of each food item plotted against its percent occurrence. Bivalves and flesh accounted for a large proportion of stomach contents of the smallest lobsters (7-mm-CL size class) and were found in ≥75% of stomachs, making them the most important food items for this grouping. Rock crabs, amphipods, and polychaetes contributed 0.2 to 0.4 of stomach volume when they were ingested, but were found in fewer than 30% of the stomachs. Macroalgae and gastropods, on the other hand, were eaten by >50% of small lobsters but were ingested in small volumes. All other prey categories contributed little to stomach volume and were found in a small proportion of stomachs.

Flesh and bivalves were also the most important food items for the 10–20 mm CL lobster grouping (Fig. 4). They accounted for 0.46 and 0.22 of stomach volume, respectively, when they were ingested, and were found in 90% of stomachs. Rock crab was another important prey, with a specific abundance of 0.32 and an occurrence of 41%. Pagurids, carideans, and echinoderms had high specific abundances but were found in less than 5% of stomachs. Gastropods and polychaetes were found in about 40% of stomachs, but accounted for a small fraction of stomach volume. All other prey categories constituted a small fraction of the volume of very few stomachs.

The two main food items of lobsters measuring 25–60 mm CL were rock crab and flesh: specific abundance was high (0.34 and 0.38, respectively) and these food items

Table 2

Major categories of food items, divided into specific food items when possible, and their overall volumetric contribution (total=1) to stomach contents of all examined lobsters from Baie de Plaisance, Magdalen Islands. Abbreviations for major categories of food items are shown in brackets.

Categories of food items	Volumetric contribution
Formaniferans [For]	0.0031
Macroalgae [Alg]	0.0394
Coralline algae (*Corallina officinalis*) [Cor]	0.0178
Hydrozoans [Hyd]	0.0207
Bivalves [Biv]	0.1657
Mytilus edulis	0.0202
Modiolus modiolus	0.0992
Unidentified Pelecypoda	0.0463
Gastropods [Gas]	0.0585
Lacuna vincta	0.0028
Unidentified Gastropoda	0.0057
Polychaetes [Pol]	0.0597
Nereidae	0.0318
Polynoidae	0.0271
Unidentified Polychaeta	0.0008
Barnacles (*Balanus* sp.) [Bar]	0.0012
Crustacean meiofauna [Cru]	0.0053
Harpacticoida	0.0003
Ostracoda	0.0021
Unidentified minute Crustacea	0.0029
Amphipods [Amp]	0.0054
Corophium sp.	0.0004
Gammarus sp.	0.0003
Caprellidea	0.0004
Gammaridae	0.0016
Unidentified amphipods	0.0027
Isopods [Iso]	0.0067
Idotea sp.	0.0013
Idoteidae	0.0019
Unidentified valviferan isopods	0.0034
Carideans [Car]	0.0024
Crangon septemspinosa	0.0010
Unidentified carideans	0.0013
Pagurids [Pag]	0.0416
Pagurus acadianus	0.0051
Paguridae	0.0365
Rock crab (*Cancer irroratus*) [Cra]	0.2637
American lobster (*Homarus americanus*) [Lob]	0.0076
Echinoderms [Ech]	0.0222
Strongylocentrotus droebachiensis	0.0102
Ophiuroidea	0.0012
Unidentified echinoderms	0.0109
Fish [Fis]	0.0066
Flesh [Fle]	0.2724

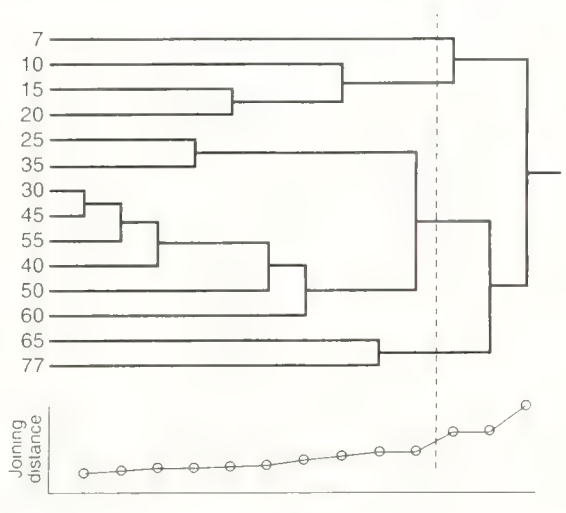

Figure 2

Dendrogram resulting from a cluster analysis on the mean volumetric contribution of major food categories by size class of lobsters from the Magdalen Islands. The bottom graph shows the joining distance at each step. The vertical dashed line indicates the cut-off value for clusters, selected because of the sudden increase in joining distance.

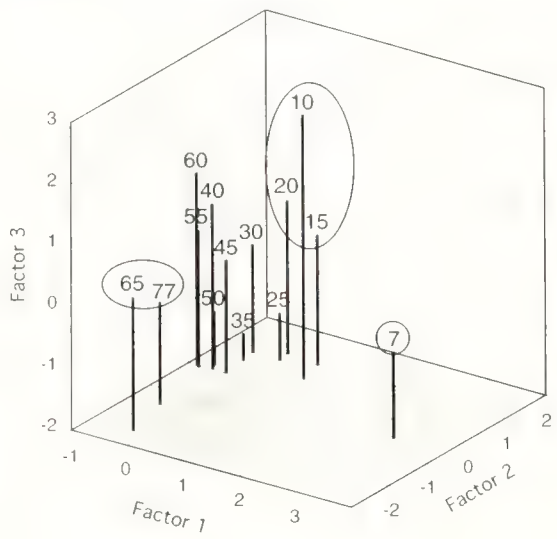

Figure 3

Results of the factor analysis on the correlation matrix of volumetric contribution of major food categories by size class of lobsters from the Magdalen Islands. See text for factor loadings. Three clusters identified in Figure 2 are shown inside ellipses; the other size classes constitute the fourth cluster.

were found in more than 70% of stomachs (Fig. 4). Bivalves were still found in a large proportion of stomachs (87%) but accounted for a low proportion (0.18) of volume. Gastropods, polychaetes, and macroalgae also occurred frequently but accounted for only a small fraction of stomach volume. Pagurids and lobsters were found in few stomachs but contributed >0.2 of stomach volume.

The grouping of the largest lobsters, 65–77 mm CL, had rock crab as the most important food item (specific abundance=0.55; occurrence=86%). Lobsters, pagurids and fish contributed a large proportion of stomach volume when they were eaten, but these prey were ingested by <20% of lobsters. Gastropods, flesh, bivalves, polychaetes, and macroalgae were found in a large proportion of stomachs but occupied a small proportion of the volume of these stomachs.

Overall, bivalves, rock crab, and flesh were the only food items that each accounted for >0.1 of stomach volume for the whole sample (Table 2). For these food items, a significant linear relationship existed between volumetric contribution and lobster CL, the latter explaining 68% to 92% of the variability in volume (Fig. 5). Regression of volumetric contribution on lobster CL produced a negative slope for bivalves and flesh, and a positive slope for rock crab. Similarly, strong linear or nonlinear relationships existed between percent occurrence of these three food items and lobster CL (Fig. 5). Furthermore, large lobsters tended to eat larger rock crabs than small lobsters, as evidenced by the significant positive linear relationship between the CW of rock crabs found in lobster stomachs and lobster CL (Fig. 6).

Discussion

Data

Stomach content analysis is a useful method for the investigation of the natural diet of animals, even though the lack of distinctive hard parts in some prey and differential digestibility of soft and hard body parts limits the spectrum of food items that can be recognized and can lead to biased perception of the relative importance of the food items. We took care to process lobsters as quickly as possible after collection, thus attenuating the effects of differential digestibility, and we examined only intermolt and nonovigerous lobsters, thus reducing sources of diet variability associated with molt cycle and female reproductive status (e.g. Weiss, 1970; Ennis, 1973). In addition, our study was conducted over a small area where the various lobster size classes were evenly distributed; therefore all lobsters potentially could access the same food. We recognize that our volumetric contribution index underestimates the importance of predominant food items, owing to correction for stomachs with multiple food items and total scores >10. However, this was a minor problem because analyses using uncorrected values revealed that the volumetric contribution of the three main food items was underestimated by no more than 2–5% and that relationships to lobster size class were unchanged. Therefore, we are confident that the dietary differences among the lobster size classes that we detected are real and that they

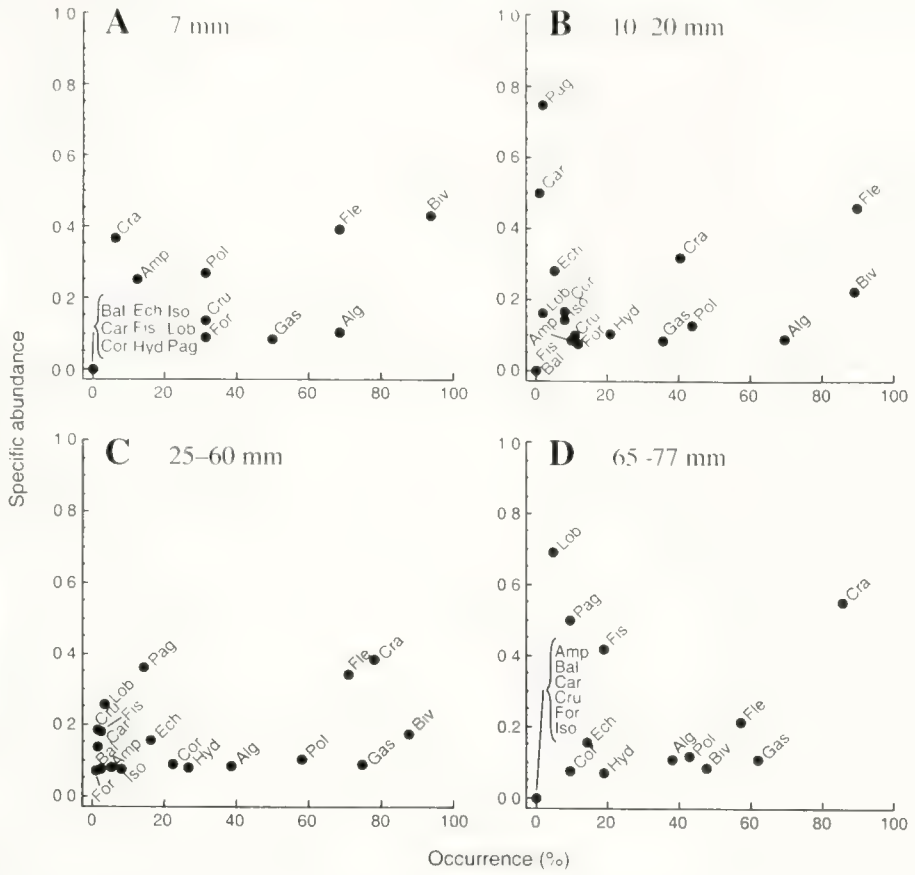

Figure 4

Relationship between specific abundance and percent occurrence for the major food categories in relation to clusters for size classes of the (**A**) 7 mm, (**B**) 10–20 mm, (**C**) 25–60 mm, and (**D**) 65–77 mm CL (see Fig. 2) for lobsters from the Magdalen Islands. Refer to Table 2 for abbreviations of major food categories.

reflect mainly changing lobster preferences and differential accessibility of prey types.

Ontogenetic shifts in diet

There was clear evidence of a progressive dietary shift with increasing lobster size at our study site. Smaller lobsters relied to a greater extent than larger lobsters on soft or easily acquired food items (flesh, sessile juvenile bivalves, macroalgae, meiobenthic crustaceans, and foraminiferans). Larger lobsters fed on bigger, more mobile and also more nutritious prey, including crustaceans that were protected by heavy shells, and fish. Fishes were probably taken by predation (see Weiss, 1970) because there was no fishing activity at or near our study site that might have provided lobsters with fish bait or discards.

The most striking ontogenetic changes in volumetric contribution of prey types occurred for rock crab and bivalves, the former increasing from 0.07 to 0.53 and the latter decreasing from 0.28 to 0.02 from the smallest to the largest lobster size class, respectively (Fig. 5). Only limited comparisons with other studies are possible, given the differences in methods and in the size range of lobsters examined. However, the observed trends of increasing importance of rock crab and of decreasing importance of bivalves with increasing lobster size were consistent with the analyses of Scarratt (1980) and of Carter and Steele (1982b), and they suggest that lobsters are not simply opportunistic or unspecialized feeders (see Elner and Campbell, 1987).

Multivariate analysis of lobster diet resulted in size groupings that are quite consistent with Lawton and Lavalli's (1995) size classification of the early life-history phases based on a broad set of behavioral and ecological criteria. Major shifts in diet in the present study occurred at about 7.5, 22.5, and 62.5 mm CL (Fig. 2). The two classifications differ in the smaller size for the transition from the first to second group (7.5 mm in our diet-based classification compared with 14.5 mm CL in Lawton and Lavalli's scheme), but the size for transition from the second to the

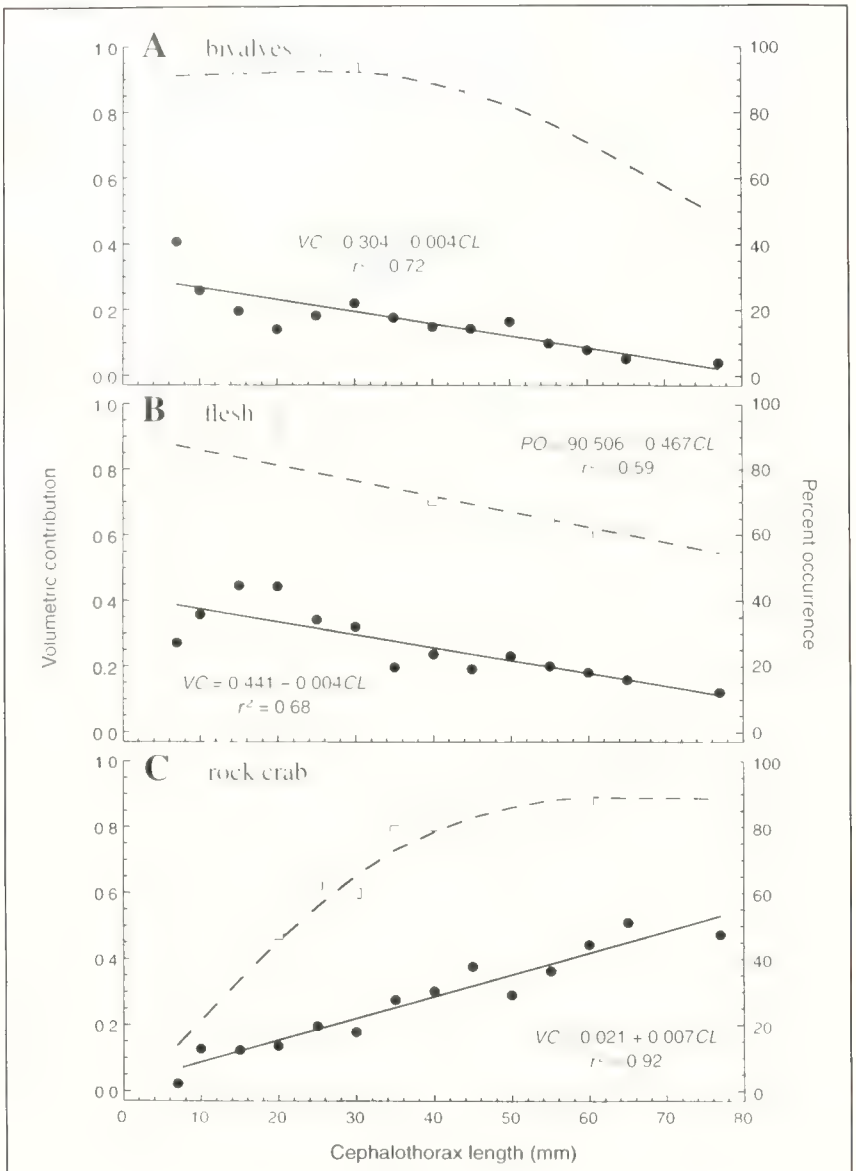

Figure 5

Relation between percent occurrence (PO, □) or volumetric contribution (VC, •) and lobster cephalothorax length for the three main food items of lobsters from Magdalen Islands: (**A**) bivalves, (**B**) flesh bolus, and (**C**) rock crab. All linear regressions are highly significant (P<0.001).

third group is the same in both studies (22.5 and ~25.0 mm CL). Comparison of the size threshold for transition from the third to the fourth group is less appropriate because Lawton and Lavalli (1995) considered this threshold to be determined by physiological maturity, which is a temperature-dependent trait that varies among regions.

Natural diet of shelter-restricted juveniles

This first investigation of the diet of SRJ lobsters does not support the view that these juveniles derive a substantial portion of their diet by suspension feeding and browsing in their shelters, at least at our study site and during the two years we sampled. With respect to suspension feeding, there was no evidence of planktonic organisms in stomachs, although some of the unidentified prey of the crustacean meiofauna category may have been planktonic. Foraminiferans, harpacticoids, ostracods, and macroalgal debris represented food items that potentially could be browsed within shelters. However, these taxa together contributed relatively little to stomach volume of lobsters in the 7-mm size class (0.14 for the combined categories,

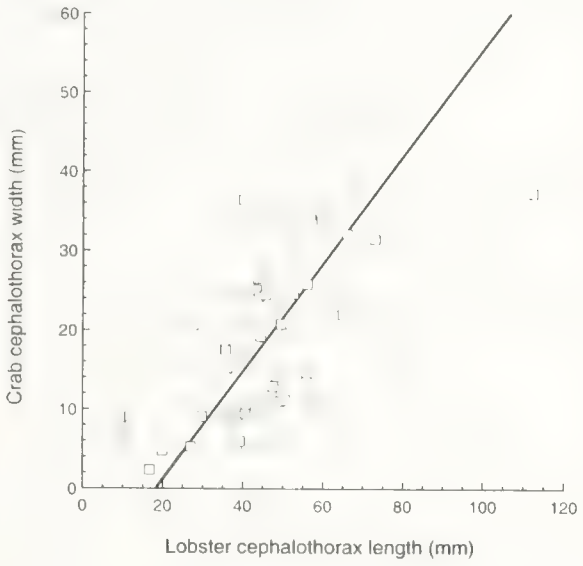

Figure 6

Relationship of predator (lobster) size to prey (rock crab) size, based on rock crab cephalothorax width (CW) estimated from measurements of indicator fragments and lobster cephalothorax length (CL), for the Magdalen Islands. Model II regression: $CW = -12.341 + 0.677CL$ [r^2=0.34, P<0.001].

in spite of the fact that one or the other category occurred in 88% of stomachs) and even less to stomach volume of lobsters in the 10-mm size class (0.10, 86%). During our study, lobsters settled in August at sizes of 4.3–5.2 mm CL and grew to 12–14.5 mm CL by October (Sainte-Marie et al., 2001). Thus, we sampled the lobster population during the only period of time when SRJs were present and seasonal sampling bias cannot be invoked to explain the lack of plankton in their diet.

The other food items in the stomachs of SRJs, and especially the predominant bivalves and flesh (Figs. 4 and 5), probably were derived by predation and scavenging. Bivalves in the stomachs of SRJ lobsters were represented by recently settled *Modiolus* and *Mytilus*. Mussel spat may settle aggregatively and quite synchronously, forming dense patches that can provide a short-term prey pool requiring little or no search time (e.g. Auster, 1988). Furthermore, because mussel spat often settle in crevices or under rocks (e.g. Nair et al., 1975), SRJs could access them with little or no risk of exposure to predators. Lawton (1987) argued that dominance and territoriality were likely to exist early in the ontogeny of lobsters, as demonstrated subsequently (James-Pirri and Cobb, 1999; Paille and Sainte-Marie, 2001), and that prolonged occupation and defense of shelters located close to a food patch would be advantageous for juveniles. Exploitation of mussel patches, inferred from the present study, is consistent with that hypothesis.

Flesh (tissue boluses) that could not be attributed to a particular animal for lack of indicator fragments was a very important food item in the diet of SRJs, both in terms of percent occurrence and of volumetric contribution (Figs. 4 and 5). Elner and Campbell (1987) also found that unidentified animal tissue was one of the most frequent and most volumetrically important foods in the stomachs, however, of larger lobsters. Weiss (1970) observed that adolescent and adult lobsters often captured crabs or other shelled prey, cracked them open, and then selectively ingested only soft tissue. Interestingly, the percent occurrence and volumetric contribution of flesh to diet was greater in lobsters of size classes ≤30 mm CL (i.e. SRJs and emergent juveniles) than in larger lobsters (Fig. 2). It is unlikely that the smallest of lobsters could find (within the confines of their shelter) and subdue prey sufficiently large to provide tissue boluses devoid of hard parts. Furthermore, claws are not differentiated into cutter and crusher forms in SRJs (Govind and Lang, 1978; Costello and Govind, 1984) and early juveniles may be incapable of breaking open shelled prey (Costello and Lang, 1979; Lawton and Lavalli, 1995). Therefore, flesh ingested by SRJs and emergent juveniles probably was obtained by scavenging animal remains. Considering that larger lobsters may hoard and bury food in or nearby their dens (Herrick, 1895; Smith, 1976; Lawton, 1987; Wickins et al., 1996), we propose that early juveniles exploit the meal scraps or food reserves of larger lobsters. Indeed, we observed that small lobsters often occupied galeries beneath, or in rock pilings nearby, the dens of larger lobsters. This is consistent with reports that odor from conspecific adults is a proximate cue for lobster settlement (Boudreau et al., 1993). Cohabitation of small lobsters with large lobsters would offer the former protection from predators and a potentially abundant, high-quality, sheltered food source, and would therefore represent a form of commensalism. The risk of cannibalism for small lobsters living in the vicinity of larger lobsters probably does not offset the benefits. Few lobster remains were found in lobster stomachs in this (Fig. 4) as in other studies (Weiss, 1970; Carter and Steele, 1982b; Elner and Campbell, 1987), and an unknown proportion of those remains may have been exuviae.

Some other rarer food items found in the stomachs of SRJ lobsters were probably taken by predation, possibly within, but more likely in the neighborhood of, the lobsters' shelters. The most important of these prey by volumetric contribution were polychaetes, comprising juvenile nereids and polynoids that are frequently found in soft sediment or on the underside of rocks, and recently settled rock crab. Similarly, amphipods and gastropods found in the stomachs of SRJs were juveniles or small species that may abound in crevices and in spaces beneath rocks.

A carnivorous, high-energy diet such as the one demonstrated for SRJs in our study would promote growth from settlement time. By contrast, Lavalli (1991) demonstrated that a diet of only diatomous algae was insufficient for extended growth and survival of early juvenile lobster. A diet of mesozooplankton sustained growth of juvenile lobsters, at least for some time after settlement (e.g. Daniel et al., 1985; Barshaw, 1989; Lavalli, 1991). However, Lawton and Lavalli (1995) pointed out that intermolt periods tended to be longer and molt increments smaller in laboratory-held,

juvenile lobsters reared on mesozooplankton than in wild lobsters, suggesting that the latter incorporated more nutritious foods into their diet.

The finding that early juvenile lobsters are primarily predators or scavengers, if confirmed by studies at other sites, has implications for the development and implementation of artificial reefs. Such structures are increasingly being considered as a means to enhance lobster productivity on traditional grounds or to expand lobster habitat onto less hospitable grounds (e.g. Gendron, 1998). The carnivorous benthic feeding mode of SRJs and of emergent juveniles at our site implies that successful reefs will have to be designed, localized, and weathered so that they are initially well colonized and subsequently regularly colonized by benthic prey that are easily accessible and of high nutritional value to juvenile lobsters. Additionally, if SRJs and emergent juveniles derive some protective and nutritional benefits from the presence of larger conspecifics, reefs designed to offer shelter to a full suite of lobster sizes may prove to be more productive in the long term than reefs offering shelter only to small lobsters.

Importance of rock crab to lobster

Several previous studies have noted the importance of rock crab in the diet of lobster (Reddin, 1973; Evans and Mann, 1977; Carter and Steele, 1982a). Boghen et al. (1982) found that juvenile lobsters survived and grew better on a diet containing crab protein alone than on a diet of live brine shrimp (*Artemia salina*) or of protein extracts from urchin (*Strongylocentrotus droebachiensis*), mussel (*Mytilus edulis*), or shrimp (*Penaeus* sp.). Gendron et al. (2001) found that condition, somatic growth, and gonadal development of lobster increased with increasing amount of rock crab in diet. In nature, even SRJs may benefit from a diet including large amounts of rock crab protein because they preyed directly on very small rock crabs (Figs. 4 and 5), and the tissue boluses they contained may have been that of rock crab (see above).

We were able to establish a positive size relationship for lobster preying on rock crab (Fig. 6). The smallest rock crab prey were 2–6 mm CW and belonged to the first benthic instars of this species. In our study, apparently no rock crabs larger than 50 mm CW were consumed by lobsters, and the maximum ratio of crab CW over lobster CL was 0.90, even though rock crabs up to 120 mm CW were seen (own personal diving observations). In the laboratory, Weiss (1970) observed that lobsters of 60–80 mm CL attacked crabs offered in the size range of 62–78 mm CW. Lawton and Lavalli (1995) reported that juvenile lobsters can subdue juvenile intermolt rock crabs up to approximately 0.40 times their own body size. Their observation was based on the comparison of predator and prey wet masses; when expressed in terms of crab CW over lobster CL, the maximum ratio was equivalent to about 1.27.[1] This ratio of prey CW to predator CL is somewhat larger than that derived from our stomach analyses. Because lobsters probably ingest only soft tissue when the prey-predator size ratio is sufficiently high (Weiss, 1970; and see above), our analysis of rock crab prey-size frequencies may correctly estimate the minimum prey size but underestimate the maximum prey size and the volumetric contribution and occurrence of rock crab in the diet of any given lobster size class. Nevertheless, the present study clearly shows that all lobster size classes rely on rock crab as food and that the size spectrum of rock crab that is used by lobsters is broad and includes even those at the settlement stage. Given the much greater economic value of lobster in relation to rock crab, and the trophic dependency of the former on the latter, caution should be exercised in developing rock crab fisheries (Gendron and Fradette, 1995).

[1] Lawton, P. 2000. Personal commun. Fisheries and Oceans Canada, St. Andrews, New Brunswick, Canada.

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Age and growth of Hawaiian green seaturtles (*Chelonia mydas*): an analysis based on skeletochronology

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Abstract–Skeletochronological data on growth changes in humerus diameter were used to estimate the age of Hawaiian green seaturtles ranging from 28.7 to 96.0 cm straight carapace length. Two age estimation methods, correction factor and spline integration, were compared, giving age estimates ranging from 4.1 to 34.6 and from 3.3 to 49.4 yr, respectively, for the sample data. Mean growth rates of Hawaiian green seaturtles are 4–5 cm/yr in early juveniles, decline to a relatively constant rate of about 2 cm/yr by age 10 yr, then decline again to less than 1 cm/yr as turtles near age 30 yr. On average, age estimates from the two techniques differed by just a few years for juvenile turtles, but by wider margins for mature turtles. The spline-integration method models the curvilinear relationship between humerus diameter and the width of periosteal growth increments within the humerus, and offers several advantages over the correction-factor approach.

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The Hawaiian population of the green seaturtle (*Chelonia mydas*) provided some of the first published growth data (Balazs, 1979, 1980, 1982) for this species. These early data showed how slowly seaturtles grow and how long a female must survive simply to lay her first clutch of eggs. Twenty or more years to reach sexual maturity seemed biologically unrealistic, yet slow growth and late maturity has been repeatedly confirmed for some seaturtle species, e.g. Bahamian *C. mydas* (Bolten et al., 1992), West Atlantic *Caretta caretta* (Parham and Zug, 1998). Slow growth and the resulting delayed maturity greatly affect the demography of a population (Crouse et al., 1987; Chaloupka and Musick, 1996). An understanding of growth and growth-pattern variation in seaturtles is an important prerequisite to the development of population models that are required to guide seaturtle population recovery and conservation.

Green seaturtles within the Hawaiian Islands contribute to the larger Indo-Pacific *C. mydas* gene pool, yet the nesting females of the Hawaiian population comprise a distinct genetic unit and contain a unique mtDNA haplotype (Bowen et al., 1992). Except during their posthatching pelagic phase, the great majority of Hawaiian green seaturtles reside in coastal waters, primarily around Hawaii, Kauai, Maui, Molokai, Oahu, and other islands in the southeastern part of the Hawaiian chain. Most reproduction takes place at French Frigate Shoals in the Northwestern Hawaiian Islands (Balazs, 1980; Wetherall et al., 1999). The population of Hawaiian *Chelonia mydas* has benefited from over two decades of intense conservation management (Balazs, 1998). Despite important early research on the Hawaiian population of *C. mydas* (Balazs, 1982), the patterns of growth within and among the geographic habitat components of this population have remained incompletely documented (Balazs et al., 1994, 2000). The chief reason for this has been a lack of methods to age sea turtles. This deficiency has been overcome recently by the development of skeletochronological techniques that estimate age from the number of growth increments formed on the humerus (Parham and Zug, 1998).

Our goal in this study was twofold. First, we used humerus growth-increment data to estimate ages of a sample of Hawaiian green seaturtles from various locations in the archipelago and developed a growth model for the general Hawaiian population; geographic variation in growth will be addressed in a subsequent paper. Second, we compared two different methods of deriving the age estimates, the so-called "correction-factor" method described by Parham and Zug (1998) and a newer approach, the "spline-integration" method, introduced in the present study.

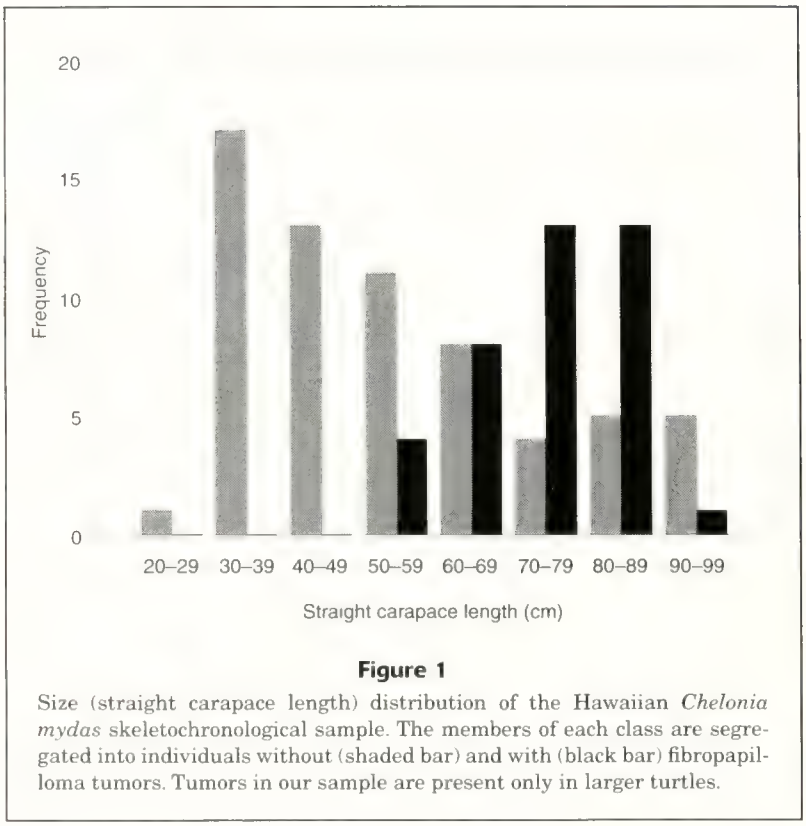

Figure 1

Size (straight carapace length) distribution of the Hawaiian *Chelonia mydas* skeletochronological sample. The members of each class are segregated into individuals without (shaded bar) and with (black bar) fibropapilloma tumors. Tumors in our sample are present only in larger turtles.

Materials and methods

Our sample consisted of 104 individuals of *C. mydas*, collected from the islands of Hawaii, Kauai, Lanai, Maui, Oahu, and the Northwestern Hawaiian Islands; the Oahu sample predominated with 64 individuals. All individuals were measured to the nearest 0.1 cm straight carapace length (SCL). The smallest individual was a 5.3-cm-SCL hatchling. The smallest posthatchling was a pelagic juvenile (of assumed Hawaiian origin) recovered from the former squid driftnet fishery north of the island chain. All other posthatchling turtles were from coastal Hawaiian waters, found stranded dead and retrieved by the National Marine Fisheries Service's Hawaiian Islands Seaturtle Stranding Network. The salvaged turtles ranged from 28.7 to 96.0 cm SCL. The sample was divided into eight 10-cm size classes; representation was roughly equivalent for the middle six classes (Fig. 1). The 30–39 cm sample contained only turtles in the upper quartile of this size class. Each turtle was necropsied and its right humerus removed for skeletochronological examination. The necropsy data included a complete set of carapace measurements, organ condition evaluations, and information on fibropapilloma tumor occurrence and severity; see Work and Balazs (1999a, 1999b) for details on the entire data set. In addition to the skeletochronological data, we used only the SCL measurements and tumor-evaluation observations in the present study.

Where possible, we selected tumor-free individuals for the present analysis because our goal was to examine the overall growth pattern for normal Hawaiian *Chelonia mydas*. Because the prevalence of fibropapillomatosis is high in the wild Hawaiian population (Murakawa et al., 2000), we included in our sample individuals with fibropapillomas, but otherwise appearing normal, in order to ensure adequate representation in the larger size classes. Healthy animals were those showing no evidence of weight loss or other indicators of illness and no evidence of disruption or retardation of normal growth. Individuals with tumors represented 27% of the 50–59 cm, 50% of 60–69 cm, 76% of 70–79 cm, 73% of 80–89 cm, and 17% of 90–99 cm SCL size classes (Fig. 1).

Our skeletochronological data derived from cross-sections (0.6–0.8 mm thick) from the middle of the humeral shaft just distal to the deltopectoral crest and at the narrowest diameter of the diaphysis (Zug et al., 1986). On each specimen, we counted the number of visible growth layers and measured the widths (long-axis diameters) of the humerus at each successive growth cycle and the width of the resorption core. Bone sections were taken from mid-shaft, the narrowest location of the bone, because the humerus retains the greatest number of periosteal growth layers there, and hence this location permits the most accurate estimation of the number of growth cycles (periosteal layers) and the relative rates of growth (=successive humerus diameters).

We used two procedures for estimating the total number of growth layers, and hence age, of each turtle. In the correction-factor (CF) method, as described in Parham and Zug (1998), the turtle's age is estimated as the number of growth layers observed in the outer region of the humerus section plus the predicted number of resorbed growth layers represented in the remodeled core of the humerus. The latter, unobservable component is estimated as $C\,(R - R_H)$, where R is the radius of the absorption core, R_H is the radius of a hatchling's humerus (before the beginning of increment formation), and C is the so-called correction factor. The correction factor is a constant "aging rate" (yr/mm) assumed to apply to the resorption core, and calculated as the reciprocal of the mean growth layer width in small turtles. The mean growth layer width was estimated from 129 periosteal growth layer widths observed in 34 turtles

with SCLs <60 cm and resorption core diameters <19.0 mm. Selecting only small turtles with minimum core diameters reduces the frequency of the narrower periosteal layers found in the outer margin of the humerus in larger turtles; hence, it reduces the possibility of overestimating the number of layers in the resorption core. The resulting correction factor was used to estimate the number of resorbed periosteal layers.

A second method, spline integration (SI), is introduced here. The SI method uses a scatterplot smoothing spline (Härdle, 1990; Hastie and Tibshirani, 1990) to model the relationship between the aging rate and humerus diameter. Once the aging function is estimated, a turtle's age is estimated by integrating the spline over the total diameter of the turtle's humerus section. The method of modeling increment width patterns in hard parts and of estimating age by the integration of the resulting aging function was first formalized by Ralston and Miyamoto (1983) for a Hawaiian snapper and first applied to seaturtles by Zug et al. (1995). In those applications, the aging rate was a parametric function of size. In our analysis, we modeled the aging rate nonparametrically by fitting a smoothing spline to pairs of observations of growth-layer width and humerus diameter. The SI approach uses the same source of data as the CF method but without selection. Lines of arrested growth (LAG) delimit each observable growth layer. Increment width is measured as the difference between the humerus diameters at the outer LAG and the inner LAG. Assuming an increment represents one year of growth, each increment width measurement provides a measure of the humerus growth rate (mm/yr) and its reciprocal, a measure of the aging rate (yr/mm) at the observed humerus diameter (the mean diameter of the pair of LAGs). The skeletochronological sample yielded 269 such observations of aging rate and humerus diameter. The aging rates were grouped in 1-mm intervals of humerus diameter and averaged. A cubic smoothing spline was fitted to the mean aging rates by using S-PLUS (MathSoft, Inc., 1999). The age (yr) of each turtle was estimated by integrating the aging spline from its origin to the observed outside diameter of the humerus section.

To assess the effect of estimation method on age estimates, the data were divided into 10-cm SCL groups. Within each group a Student's t statistic was used to test the hypothesis that the two methods give equal age estimates.

Nonparametric growth models were estimated based on the CF- and SI-derived age estimates and associated carapace lengths, by using the same S-PLUS procedure employed for the SI-method aging spline. The validity of the growth models was judged qualitatively by comparing growth predicted by the models with observed growth in a sample of 171 Hawaiian green turtles tagged and recaptured in waters around Molokai (Balazs et al., 1999).

To assess uncertainty in the SI-based growth curve, the 269 pairs of aging rate and mean humerus diameter data were resampled 100 times, and the SI procedure applied to each bootstrap replicate data set. The 100 aging curves derived in this manner generated a bootstrap distribution of estimated age for each turtle. Nonparametric growth curves were then fitted to each derived data set, producing bootstrap distributions of predicted mean length at age. Empirical confidence intervals for the predicted mean length at age were approximated by using percentiles of the latter bootstrap distributions.

A linear regression of SCL on outside humerus diameter was estimated for the 104 sample turtles. The slope of the linear predictor was applied to the 269 humeral increments to estimate a corresponding set of carapace increments, presumed to represent annual growth. These growth rate estimates were summarized in box plots over 10-cm intervals of SCL. Mean growth rate as a function of estimated age was also estimated by computing finite differences of the SI-based growth model.

Results

Patterns in humerus growth and aging

Carapace length has a strong linear association with humerus diameter (Y=0.643 + 2.326X [where Y=SCL cm; X=humerus diameter mm], r^2=0.98, P<0.001, n=104 including the hatchling). Humerus growth-increment width, on the other hand, is nonlinearly associated with humerus diameter at the point of growth (Fig. 2). Specifically, growth increments tend to be larger when the turtles are smaller (i.e. at smaller humerus diameters) and decline as the turtles grow. Variation in humerus increment width (growth rate) shows the same pattern. The estimated aging rate, as the reciprocal of growth rate, increases as the turtles grow. The aging rate does not increase uniformly (Fig. 3). Rather, it increases gradually in small turtles, plateaus over a broad range of length for mid-size turtles, increases abruptly as turtles approach maturity, and maintains an increased rate as the mature turtles grow.

Age and growth-rate estimates

In the CF-method analysis, the correction factor, C, was estimated as 1.14 yr/mm. The resulting age estimates range from 4.1 to 34.6 yr (n=70; excluding the hatchling with age zero). The smallest turtle in the sample had the lowest age estimate and the two largest turtles, the highest estimates. Only 68% could be aged by the CF method. Skeletochronology requires a pattern of distinct layering within the bony element examined. Such patterns are most evident in the smaller, presumably younger, individuals, and the frequency of individuals with distinct periosteal layers decreases as body size increases. In selecting specimens for the CF analysis, growth layers were sufficiently distinct to estimate the number of resorbed layers, and hence the age, in decreasingly fewer turtles: 89% of turtles in the 30–69 cm SCL group, 72% in the 70–79 cm group, 18% in the 80–89 cm group, and 29% in the >89 cm group were used in the CF analysis. Of the individuals for which we were unable to obtain an estimate of resorbed layers, a nearly equal number (48%) had fibropapillomas. The prevalence of tumors for the CF-aged subsample (31%) was somewhat less than in the total sample (37%). Importantly, the tumor prevalence in the subsam-

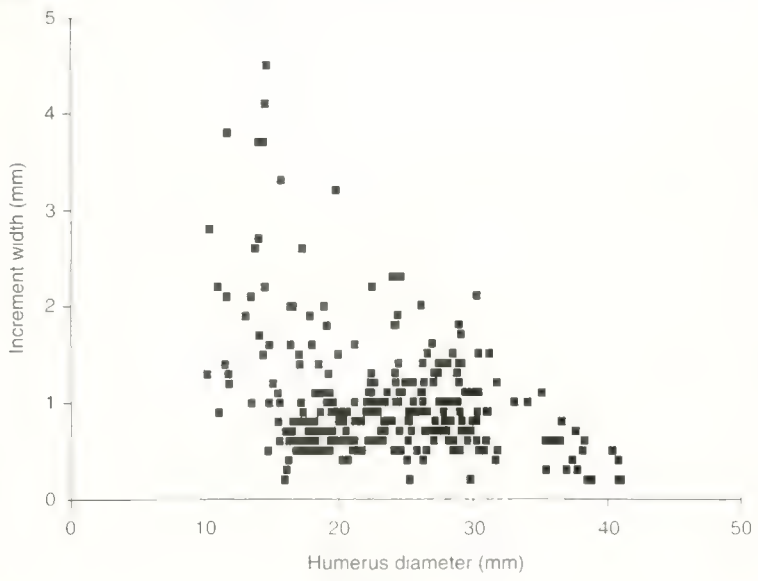

Figure 2

Humerus growth increment width (the increase in humerus diameter) in relation to humerus diameter (mean of the inner and outer diameters). Mean diameter better reflects the size of the humerus during the entire growth interval than does outer diameter.

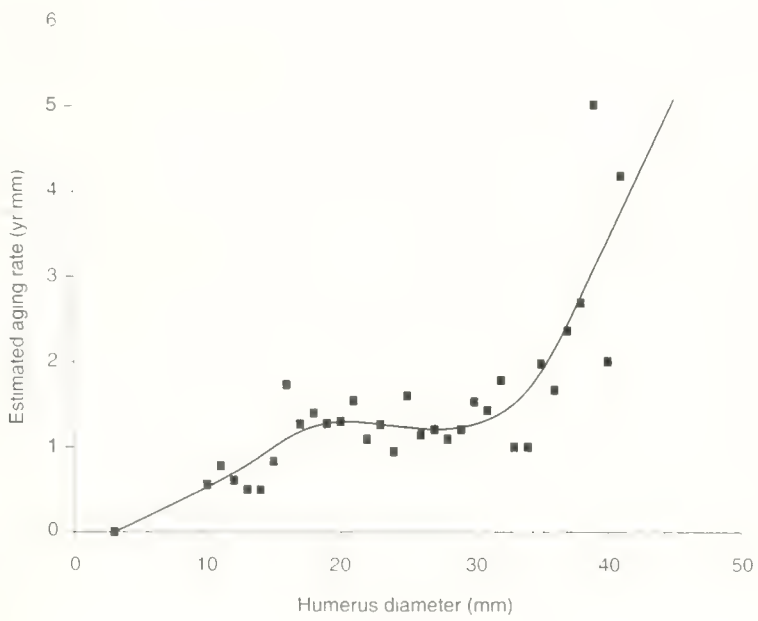

Figure 3

Estimated "aging rate" (average of the reciprocals of the humerus growth-increment widths) in relation to humerus diameter and a fitted smoothing spline. The expected age at a given humerus diameter is obtained by integrating the spline up to the specified diameter. Not all members of the sample could be aged by the CF method; see explanation in "Materials and methods" section.

ple retained for CF analysis and the subsample excluded from analysis were not significantly different (chi-square test of homogeneity χ^2=2.80, 1 df). A nonparametric growth model was estimated by fitting a scatterplot smooth to the carapace length and estimated age data (Fig. 4A). Because the CF method could not be applied to the largest turtles in the sample, the model provided no information about growth in mature turtles.

Age estimates for posthatchling turtles based on the SI method range from 3.3 to 49.4 yr (n=103). The nonparametric growth model for these data fitted very well (Fig. 4B), a result not unexpected given the dependence of the SI age estimate on humerus diameter and the tight linear relationship between humerus diameter and carapace length. Variation in carapace length around the SI growth model reflected only variance in the linear relationship between carapace length and humerus diameter; it did not incorporate variance in the age of turtles at a fixed humerus diameter or estimates of their age. The bootstrap distributions of age estimates for the SI method suggested that age estimates for a turtle can vary by up to 10 years (Fig. 5A). Nevertheless, the nonparametric confidence intervals for predicted mean length at age were narrow (Fig. 5B).

Although the CF and SI methods yielded different estimates of age (Fig. 4), over a wide range of carapace lengths, the differences were not striking. The magnitude and direction of differences in age estimates depend on SCL. Judging from the fitted smooth curves, for turtles up to about 81 cm SCL, the correction factor method was expected to give estimates of age up to 2 years higher than those produced by the spline-integration method. For larger turtles, however, age estimates derived from the correction-factor method were predicted to be as many as 10 years (or more) lower than those generated by spline integration (Fig. 6). The t-tests (Table 1) indicated there were highly significant differences in age estimates between methods within the 40–50 cm size group (t=4.36, 9 df) and the 50–60 cm group (t=4.66, 12 df). Differences for the 30–40 cm, 60–70 cm, and 70–80 cm size groups were nonsignificant; samples were too small for comparisons in other size groups.

The Molokai mark-recapture data allowed a visual comparison of observed growth and growth predicted by the CF and SI models derived from skeletochro-

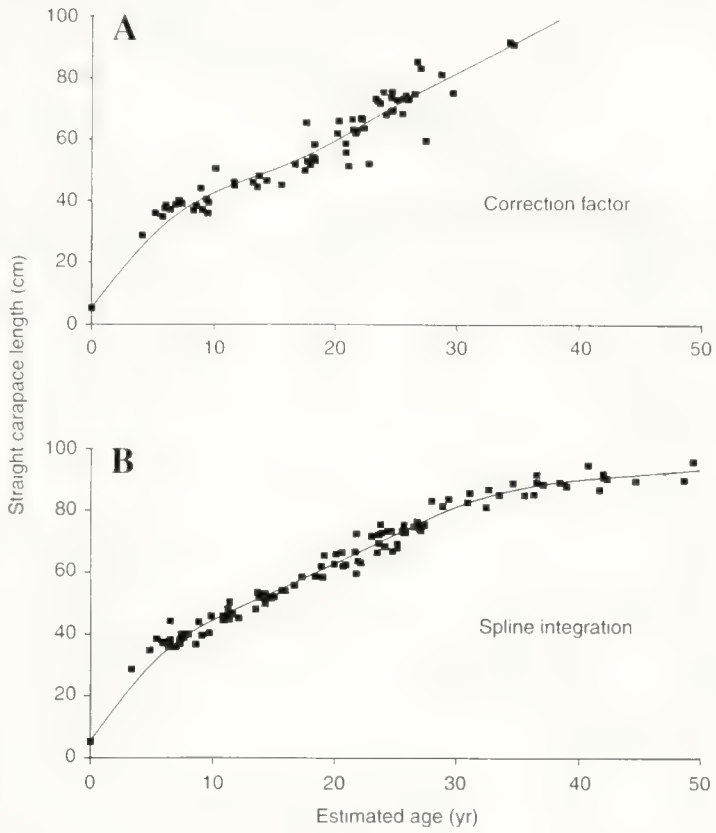

Figure 4

Relationship between observed carapace length and estimated age (squares) for the two methods of age determination: correction factor (**A**) and spline integration (**B**). Fitted growth models (curves) are cubic smoothing splines.

Table 1

Mean age estimation for correction-factor and spline-integration methods for 10-cm length groups. Estimates of mean age vary significantly between estimation methods for turtles in the middle length groups. ** indicates a significant difference.

Length group (SCL, cm)	Sample size	Mean age estimate (yr)		
		Correction-factor method (CF)	Spline-integration method (SI)	t [df], P
30–40	14	7.3	6.9	1.09 [13], 0.296
40–50	10	12.9	11.0	4.36 [9], 0.002
50–60	13	19.1	15.8	4.66 [12], 0.001
60–70	14	22.1	22.1	−0.06 [13], 0.952
70–80	13	25.3	25.6	−0.67 [12], 0.514

nological data (Fig. 7). In plotting the growth vectors for marked (tagged) turtles, we fixed the origin of each vector by assuming that the carapace length at time of first capture was given exactly by the CF- or SI-based growth curve. The observed length at recapture and time at liberty then determined the endpoint coordinates of the growth vector. Despite considerable variation in the observed growth of the marked turtles, the growth vectors were generally concordant with the growth model predictions (Fig. 7).

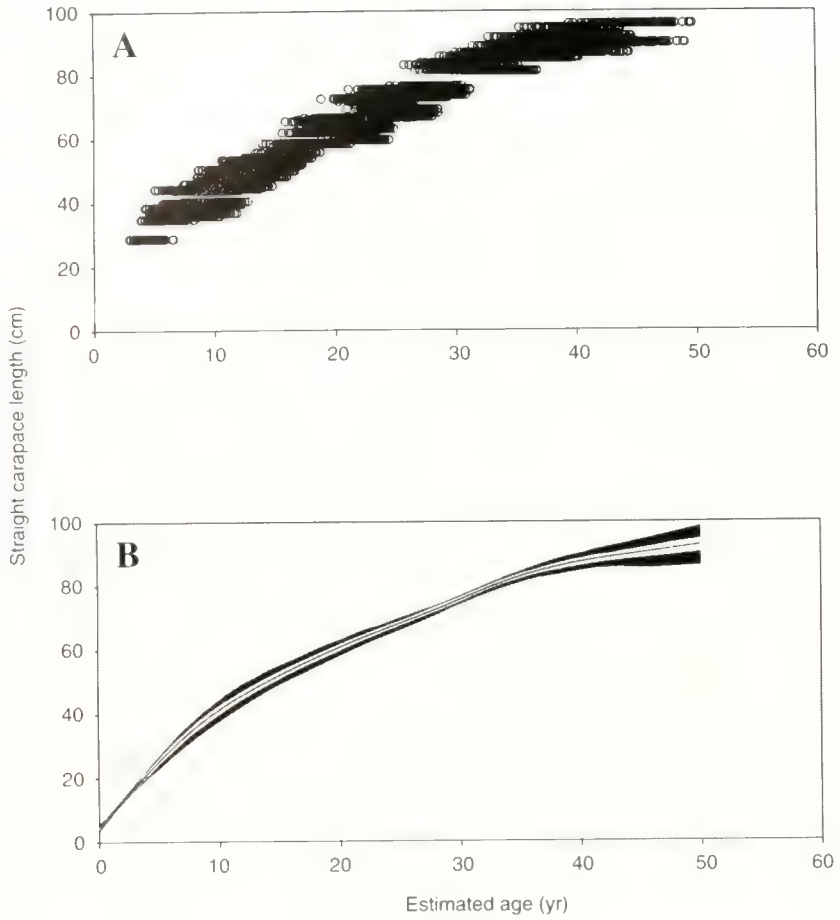

Figure 5

(**A**) Bootstrap distributions of estimated age at observed SCL generated by resampling the data for aging rate to humerus diameter 100 times and by applying the spline-integration method to each bootstrap replicate. (**B**) Corresponding distribution of growth curves, described by the bootstrap mean growth curve (line) and the approximate 50% and 95% confidence intervals for predicted mean length at age (outer and inner edges of solid region).

Age- and length-specific growth rates

The box plots of the SI-estimated carapace growth rates (Fig. 8) indicated relatively fast growth for smaller turtles, a reduced growth rate remaining fairly constant over intermediate length classes, and declining growth rates in larger, mature turtles. Mean carapace growth rate declined from 4.4 cm/yr for turtles in the 20–30 cm SCL group to less than 1 cm/yr for mature turtles in the 90–100 cm group, and remained around 2.0–2.5 cm/yr for immature juveniles in the intermediate length groups (Table 2, Fig. 8). Differences in mean growth rate among the intermediate length groups were not significant. The average growth rates predicted by first differences of the SI-based growth model (Fig. 9) indicated a similar pattern, as expected, showing a decrease in growth rate during the first decade of life (when Hawaiian green turtles are still foraging in the open ocean or in the early years of their residence in inshore habitats), relatively constant growth during the next 15–20 year interval, and a further decline in growth rate as the turtles approach 30 years of age. The growth rate appears to remain low in older turtles.

Discussion

Age and growth-rate estimates

Age estimates by both methods indicate an age range of 4–49 years for the Hawaiian green seaturtles in their coastal habitats. The pelagic juvenile (28.7 cm SCL) in our sample was about four years old (4.1 and 3.3 yr by CF and SI methods, respectively). The smallest juveniles (35–37 cm SCL) in coastal waters were 6 to 9 years old by the CF

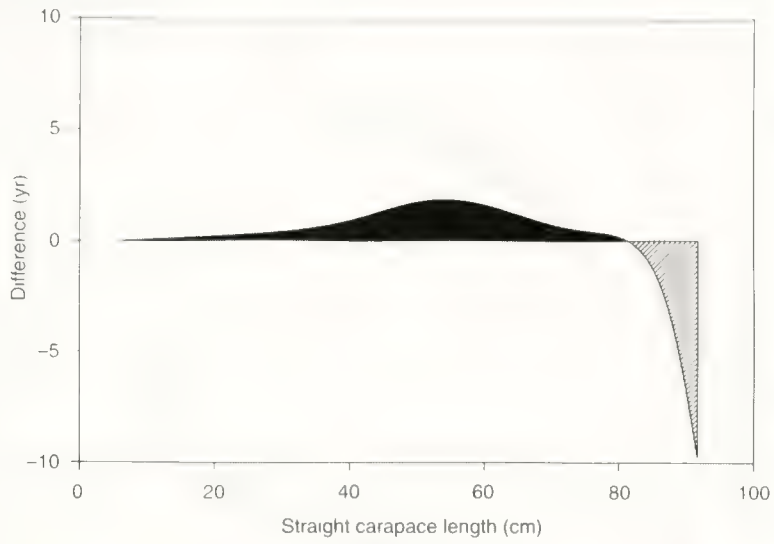

Figure 6

Difference in estimated age (yr) between the correction-factor method and the spline-integration method within the comparable range of carapace lengths (SCL). For positive values (black region), the CF method gives older ages and for negative values (striped region), younger ages.

method and 4 to 10 years old by the SI method. These age estimates for Hawaiian greens in the last years of their pelagic developmental stage are similar to those reported for *C. mydas* populations in the southern Great Barrier Reef (SGBR) (5–6 yr; Chaloupka et al., in press) and for the Atlantic coast of central Florida (3–6 yr; Zug and Glor, 1999). The smallest *C. mydas* turtle in the Florida sample was 28 cm SCL (several others were less than 35 cm), whereas the smallest SGBR turtle was 38.5 cm CCL (Limpus and Chaloupka, 1997) and the smallest Hawaiian specimen was 34.8 cm SCL, indicating an earlier shift from pelagic to benthic life in Florida greens.

The growth of the juvenile turtles predicted by both CF and SI models is consistent with the growth observed in the Molokai mark-recapture sample, but predictions of the CF model depart from the tag-recapture results in older turtles (Fig. 6). Mean growth rates for smaller (30–60 cm) turtles estimated from our transformed humerus increment data (Table 2) were about half as high as growth rates reported for turtles of the same size in most Atlantic and Caribbean locales (based on tagging and skeletochronology: Tables 2 and 3 in Zug and Glor, 1999). Our estimates were similar to the observed growth rates of tagged turtles in Kiholo Bay, Hawai'i (Balazs et al., 2000) and nearly twice as high as rates observed in some other Pacific samples (Galápagos, Heron Island; Tables 2 and 3 in Zug and Glor, 1999). Subsequent studies of Australian populations (Limpus and Chaloupka, 1997; Chaloupka et. al., in press) have shown a mid-juvenile growth rate more similar to our estimates; however, growth rate is associated with a growth surge in the Australian turtles over a narrow mid-juvenile length range (50–60 cm SCL). Such a spurt in growth was not evident in our SI-based growth curve, and growth rates were fairly constant in the 40–80 cm size classes (Fig. 8).

Table 2

Growth rate statistics by length class. Rates were derived from spline-integration data.

Length group (SCL, cm)	Growth rate (cm/yr)		
	Sample size	Mean	SD
20–30	9	4.4	2.2
30–40	37	3.5	2.7
40–50	67	2.1	1.2
50–60	53	2.3	1.0
60–70	62	2.2	0.9
70–80	21	2.1	1.0
80–90	12	1.3	0.5
90–100	7	0.6	0.3

Our age and growth estimates pertain to the Hawaiian population as a whole, because the sampled turtles originated from locations throughout the archipelago. Some variation in age and growth between island foraging groups is likely, given the extensive latitudinal range of the habitats and the associated variation in physical and biological parameters affecting growth (Balazs, 1982). A geographic analysis of age and growth will be the subject of a future study. Future study will also investigate the

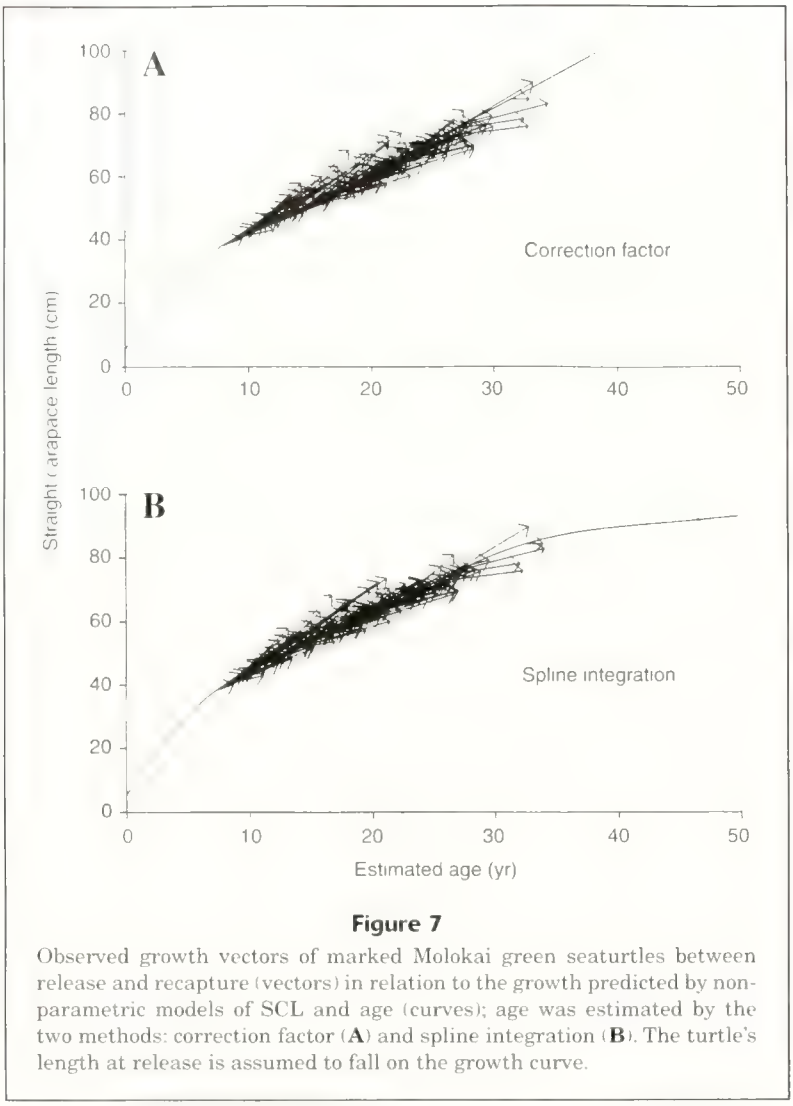

Figure 7

Observed growth vectors of marked Molokai green seaturtles between release and recapture (vectors) in relation to the growth predicted by nonparametric models of SCL and age (curves); age was estimated by the two methods: correction factor (**A**) and spline integration (**B**). The turtle's length at release is assumed to fall on the growth curve.

effects of fibropapillomatosis and gender on growth rates among the Hawaiian population.

Age-estimation methods

A key assumption of both the CF and SI methods is that each estimated humerus growth layer represents 1 year of growth. This assumption has been validated only recently (Hohn and Snover[1]). Hawaiian turtles tagged and injected with tetracycline have been recaptured, and these turtles show the appropriate number of LAGs for the years since their receipt of tetracycline. Furthermore, strong support is provided by the consistency of the growth model predictions with observed growth in tagged Molokai turtles. Additional justifications have been advanced in other studies of seaturtle humerus LAG formation (e.g. Zug and Glor, 1998; Coles et al., 2001).

[1] Hohn, A., and M. Snover. 2001. Personal commun. Beaufort Laboratory, Southeast Fisheries Science Center, Beaufort, NC.

Both the CF and SI methods require histological preparation and analysis of humerus sections. But they use the same skeletochronological data in independent and different ways to estimate the total number of humerus growth layers. The CF method assumes that a constant humerus growth rate (the "correction factor") applies to the resorption core regardless of the diameter of the core and despite the fact that periosteal increment width decreases with length of the turtle (Fig. 2). The correction factor, C, is estimated from a subset of the skeletochronological data taken from juvenile turtles only, i.e. excluding larger turtles likely to have narrower increments in the outer region of the humerus. Even so, the CF estimates of age for juvenile turtles appear to be biased upward (Fig. 5), suggesting that the constant correction factor also failed to reflect the effect of wider increments deposited in the early years of life. In age estimation, the CF method can be applied only to turtles displaying a complete set of periosteal layers, i.e. distinct LAGs, from the resorption core to the outer margin of the humerus.

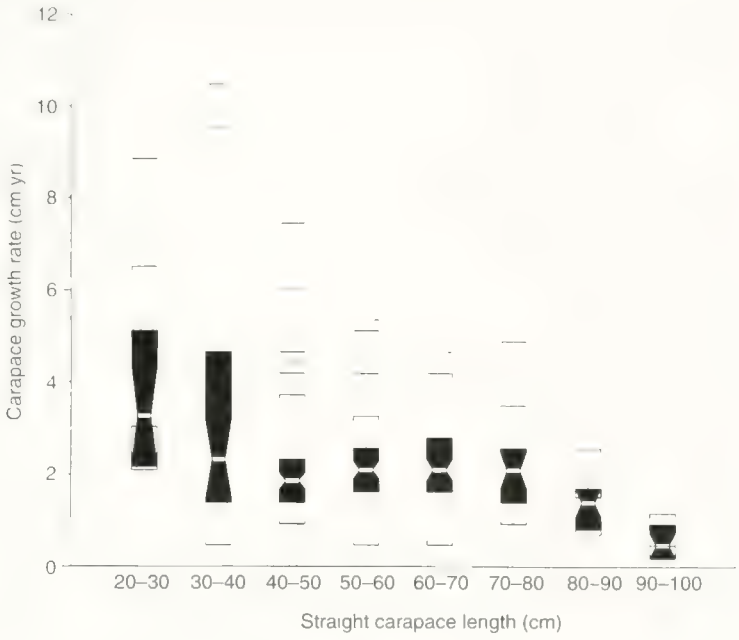

Figure 8

Variation of the growth rate estimates (SI-based) by carapace length class. Each box plot shows median (white bar), limits of 2nd and 3rd quartiles (solid notched box), range (brackets), and outliers (solid lines).

The SI method models increment-width variation over the entire distance from humerus center to outer margin by using a nonlinear, nonparametric smoother. The model is estimated from all available sample data with two or more LAGs and associated diameter measurements without regard to size of the turtle. The SI model can be applied to age all turtles for which the outside diameter of the humerus section has been measured.

In the skeletochronological sample we studied, the CF method gave age estimates significantly higher than the SI method for turtles of intermediate length (Table 1), but expected differences for such turtles were no greater than about 2 years. On the other hand, based on current data the CF-based model gives much lower age estimates than the SI-based model for turtles longer than about 86 cm SCL (Fig. 5). Thus although either method may suffice for aging juvenile Hawaiian green seaturtles, only the SI method appears to provide support for inferences about growth in turtles larger than about 80 cm. The CF method is computationally simpler, because it involves only linear regression rather than fitting and integrating a nonparametric smoother, and this consideration may recommend it to some users.

Based on our experience with Hawaiian green seaturtle data, the main issue in judging the two techniques appears to be the assumption with the CF method that humerus growth is linear. In reality, it is curvilinear, and the SI method explicitly models this curvilinearity. Moreover, the SI method makes fuller use of available humerus increment data than the CF method. Further comparisons of the methods with additional skeletochronological data sets are recommended.

Ecological précis

1 *Chelonia mydas* within the Hawaiian Islands is a component of the larger Indo-Pacific *C. mydas* gene pool, yet the nesting females of the Hawaiian population comprise a distinct genetic unit and contain a unique mtDNA haplotype (Bowen et al., 1992).

2 Except for the posthatching pelagic phase, the green seaturtles of the Hawaiian coastal waters are year-round residents, and all known individuals reproduce within the Hawaiian island chain, predominantly on the beaches of the Northwestern Islands at French Frigate Shoals (Balazs, 1998; Wetherall et al., 1999).

3 Skeletochronological age estimates indicate that Hawaiian juveniles exit the pelagic phase between the ages of 4 to 10 years.

4 In coastal waters, juveniles 10 years and older possess a relatively constant growth rate until about 28 to 30 years (approximately 80 cm SCL), then growth begins to slow as individuals attain sexual maturity.

5 The mean SCL of nesting females is 92 cm (range 81–106 cm; Balazs, 1980), suggesting ages of 30 or more years at first nesting for some individuals.

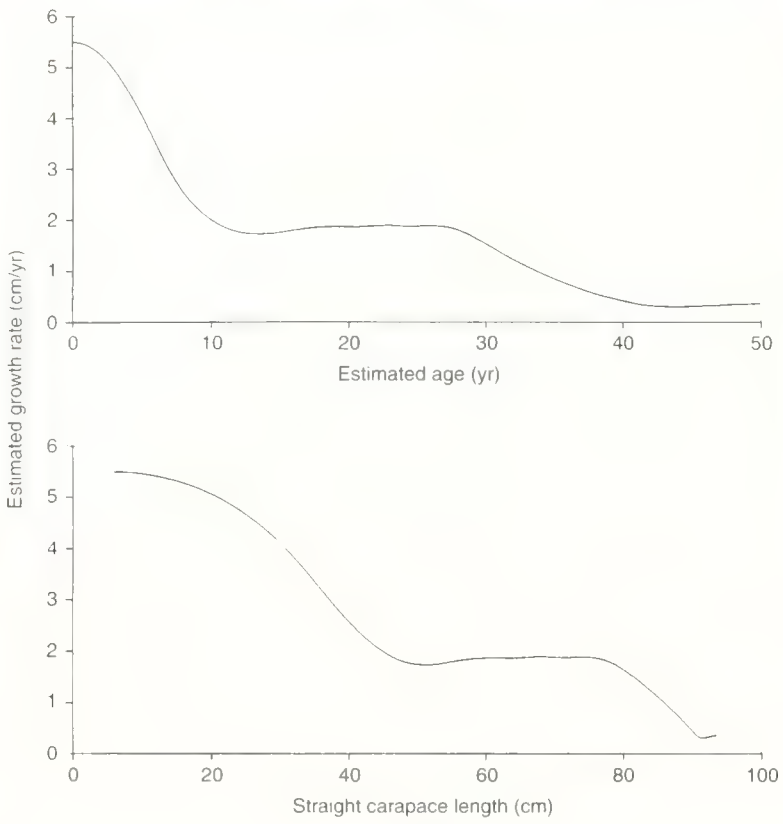

Figure 9

Growth rates of Hawaiian *Chelonia mydas* in relation to age and carapace length, estimated by taking first differences of the SI-based growth model.

Acknowledgment

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Estimates of lobster-handling mortality associated with the Northwestern Hawaiian Islands lobster-trap fishery

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The commercial lobster fishery in the Northwestern Hawaiian Islands (NWHI) is a distant-water trap fishery that targets the Hawaiian spiny lobster *(Panulirus marginatus)* and slipper lobster *(Scyllarides squammosus)*. The NWHI are an isolated group of islands, atolls, islets, reefs, and banks that extend 1500 nmi west-northwest of the main Hawaiian Islands from Nihoa Island to Kure Atoll (Fig. 1). Reported landings in the NWHI peaked at about 2,000,000 lobsters (spiny and slipper combined) in 1985, and then declined to about 38,000 lobsters from 1986 to 1995 (Fig. 2).

The NWHI lobster fishery is managed under the Fishery Management Plan for the Crustaceans of the Western Pacific Region (Crustaceans FMP) implemented in 1983 and developed by the Western Pacific Regional Fishery Management Council (WPRFMC). The National Marine Fisheries Service (NMFS) is responsible for stewardship of the resource and review and implementation of proposed management measures. A variety of management measures have been adopted in response to declining catches: a limited-entry fishing regime that limited the number of permit holders to 15; a prohibition on fishing from January through June when lobsters spawn; an annual catch quota system; a minimum legal tail width (TW) of 50 mm for spiny lobster and 56 mm TW for slipper lobster, which are close to the sizes at first maturity for these species in the NWHI; a prohibition on landing berried (ovigerous) females; and a requirement that traps be equipped with escape vents to reduce capture of undersize lobsters (WPRFMC[1]). Prior to 1996, fishermen were required to discard all berried and undersize lobsters, which were not counted against the catch quota.

The management plan assumed that escape vents allowed substantial numbers of undersize lobster to escape capture and that undersize and berried lobsters do not die during the discard process. Although research on lobster fisheries has found that escape vents effectively reduce the capture of undersize lobsters (Krouse, 1978; Fogarty and Borden, 1980; Harris, 1980; Everson et al., 1992; Skillman et al.[2]), considerable numbers of undersize (henceforth termed "sublegal") and berried lobsters are caught in the NWHI lobster fishery. Between 1983 and 1995 the reported lobster discard rate increased from 28% to 62% (Fig. 3), resulting from changes in the size- and age-structures of the populations and in the areas fished. The average size of spiny lobsters generally increased northwestward from Nihoa along the Hawaiian Archipelago (Uchida et al., 1980). Although as many as 16 banks within the NWHI have been fished, the spatial distribution of fishing effort has shifted to banks in the southeast of the Hawaiian Archipelago where there is a higher concentration of spiny lobsters.

Qualitative data collected during the early days of the fishery suggested that mortality associated with the handling and discarding practices of the NWHI commercial lobster-trap fishery might be high (Gooding, 1985; Gooding[3]). Unless discard mortality is explicitly considered, fishing policy decisions can be suboptimal, or worse. Where catch quotas are used, the total fishing-induced mortality of the population is greater than expected and can even result in recruitment overfishing. Using an equilibrium yield-per-recruit (YPR) model, Kobayashi[4] found that the reproductive potential of the NWHI lobster population more than doubled, and mean weight per individual increased by 22% in a retain-all fishery (all lobsters brought on deck were retained as catch) if the mortality rate of discarded lobsters was high (>75%). Based on these results, the observed high discard rate of sublegal and berried lobsters (62%), and the presumption that the

[1] Western Pacific Regional Management Council. 1995. Fishery management plan for the crustacean fisheries of the Western Pacific region, amendment 9. Western Pacific Regional Fishery Management Council, Honolulu, Hawaii, 227 p.

[2] Skillman, R. A., A. R. Everson, and G. L. Kramer. 1984. Prospectus escape vent experimental procedure for the spiny lobster fishery under management of the Magnuson Fishery Conservation and Management Act. Southwest Fish. Sci. Cent. Admin. Rep. H-84-13, unpubl. report, 11 p. Honolulu Lab., Southwest Fish. Sci. Cent., Natl. Mar. Fish Serv., NOAA, Honolulu, HI 96822-2396.

[3] Gooding, R. M. 1979. Observations on surface-released, sublegal spiny lobsters, and potential spiny lobster predators near Necker and Nihoa. Southwest Fish. Sci. Cent. Admin. Rep. H-79-16, unpubl. report, 8 p. Honolulu Lab., Southwest Fish. Sci. Cent., Natl. Mar. Fish Serv., NOAA, Honolulu, HI 96822-2396.

[4] Kobayashi, D. R. 2001. Southwest Fish. Sci. Cent. Admin. Rep., in prep. Simulated effects of discard mortality on spiny lobster (*Panulirus marginatus*) sustainable yield and spawning stock biomass per recruit in the Northwestern Hawaiian Islands. Honolulu Lab., Southwest Fish. Sci. Cent., Natl. Mar. Fish Serv., NOAA, Honolulu, HI 96822-2396.

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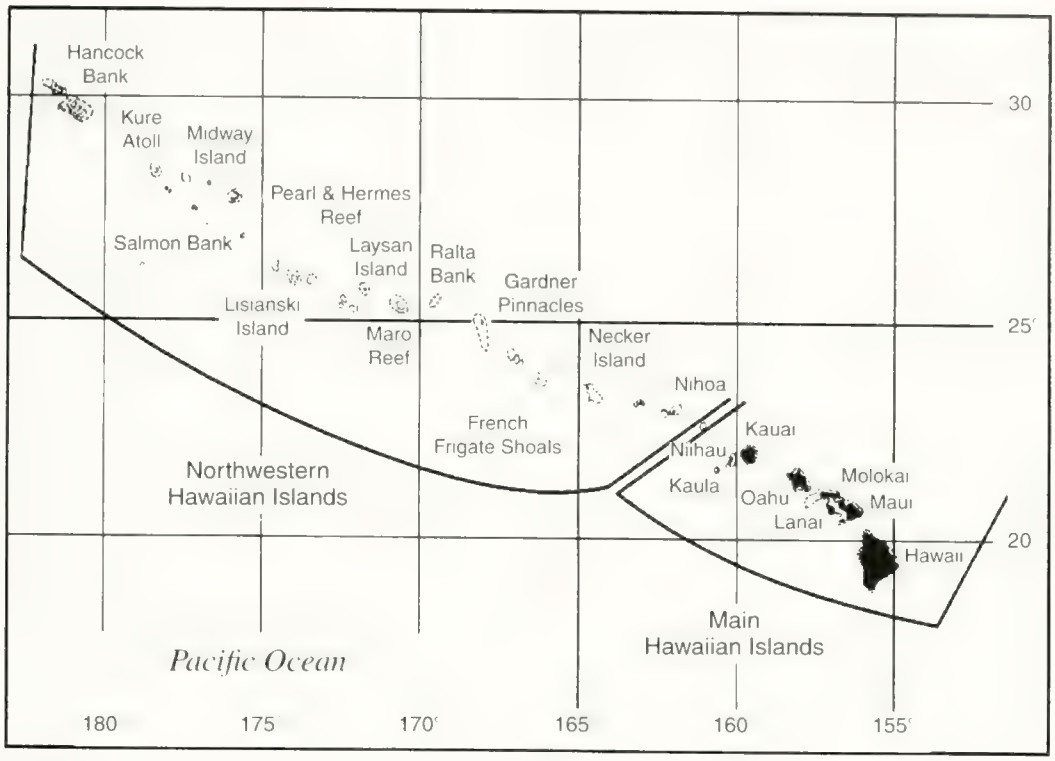

Figure 1
Map of the Hawaiian Archipelago.

Figure 2
Annual commercial landings for the NWHI lobster fishery, 1983–96.

mortality rate of discarded lobsters is greater than 75%, the WPRFMC amended the Crustaceans FMP in 1996 to allow the retention of all lobsters caught in the NWHI commercial lobster-trap fishery subject to the quota on total catch (WPRFMC[1]). The WPRFMC also recommended that NMFS conduct experiments to assess mortality associated with possible handling and discarding practices.

This study reviews research conducted in the NWHI on fishery-induced mortality of sublegal and berried lobsters. The authors examined on-deck mortality of sublegal and

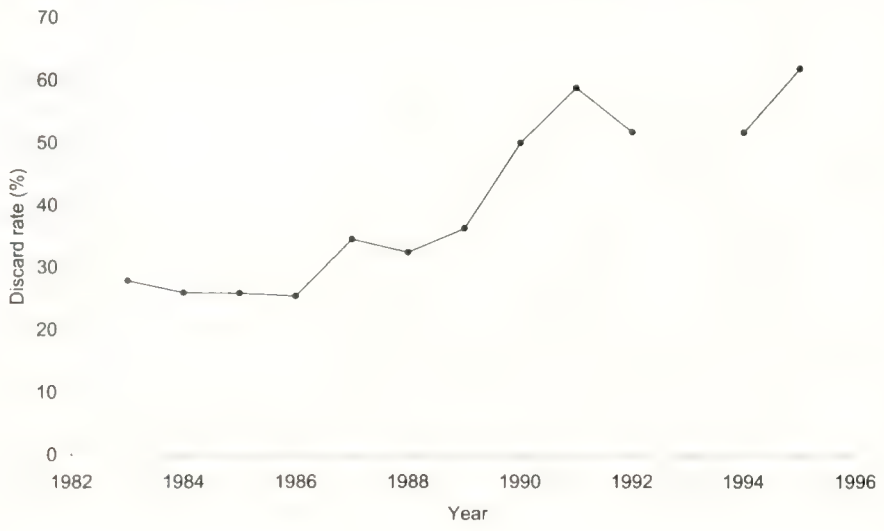

Figure 3

Annual estimates of the reported discard rate of lobsters in the NWHI lobster fishery, 1983–95.

berried spiny and slipper lobsters that occurred within two days after capture under handling methods known to have been used in the NWHI lobster-trap fishery.

Methods

Studies of handling-induced mortality (referred to as "handling mortality" in the remainder of this note) for spiny lobster were conducted at Necker Island onboard the NOAA ship *Townsend Cromwell* during the NMFS Honolulu Laboratory's 1996 NWHI lobster survey from 21 to 26 June 1996 and for slipper lobster at Maro Reef from 4 to 11 July 1996 (see Fig. 1). These locations were chosen because of their historically high lobster catches and their overall importance to the commercial lobster fishery over the past 13 years.

Handling mortalities were estimated for two handling methods: "dry" and "wet." The effects of on-deck exposure time on handling mortality were also estimated for spiny lobsters handled by the dry method. We defined a particular combination of factors (method and exposure time) as an experimental treatment. For dry treatments, lobsters were held on deck in 30-gallon containers without water and in direct sunlight for 1, 2, or 3 hours. In the wet treatment, lobsters were held on deck for 3 hours in shaded 30-gallon containers with circulating seawater. The 2- and 3-h dry treatments represent prevailing commercial fishing practices (Anderson[5]), whereas the 1-h dry treatment and the 3-h wet treatments represent possible handling alternatives or mitigative measures.

Spiny and slipper lobsters were collected in baited commercial lobster traps and sorted (legal, sublegal, and berried). All sublegal and berried lobsters were held in tanks of circulating water until a sufficiently large paired experimental treatment sample (n=200 lobsters) was collected. Experiments with the 3-h wet and dry treatments were done first, followed by experiments involving 1- and 2-h dry treatments. For each treatment, 100 lobsters (sublegal and berried) were randomly chosen from the tank and placed into two 30-gallon treatment containers (dry or wet), 50 lobsters/container. After the exposure time (1, 2, or 3 hours), lobsters were removed from the treatment containers, their condition recorded as active (i.e. lobsters were capable of tail flexion), weak (incapable of tail flexion but able to move appendages when prodded), or dead. Five lobsters were placed in each of 20 lobster-holding traps (commercial lobster traps with sealed entrances) and held in two 1320-gallon baitwells with recirculating seawater (21 gallons/minute) for 2 days. It was assumed that the 2-d holding period would allow ample time for latent effects from a treatment to manifest and that each lobster holding trap was a replicate (n=20 replicates/treatment). To check for possible baitwell effects, five control traps, each containing five previously untreated lobsters, were placed in the baitwells (two traps in the port baitwell and three traps in the starboard baitwell) at the beginning of the holding phase, and their condition was recorded at the beginning and end of the holding phase. At the conclusion of the holding period, the condition of the treated lobsters was again assessed.

Handling mortality for each treatment was computed as the arithmetic mean of the percent mortality (dead/total or (dead + weak)/total—see below) observed in the 20

[5] Anderson, P. 1997. Personal commun. University of Hawaii, Marine Option Program, 1000 Pope Road, Honolulu, HI 96822. Kazama, T. 1997. Personal commun. Honolulu Laboratory, Southwest Fisheries Science Center, 2570 Dole Street, Honolulu, HI 96822-2396.

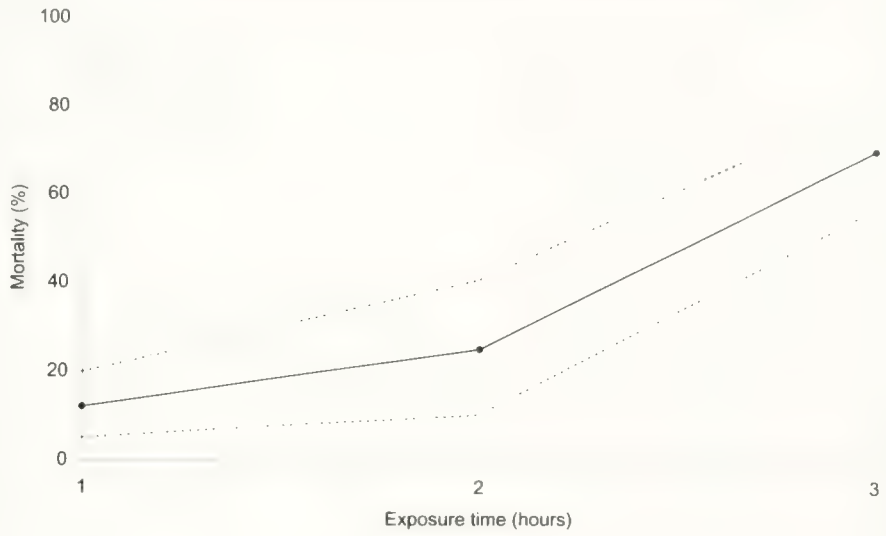

Figure 4

Handling mortality (dead/total) estimates for spiny lobster subjected to 1-, 2- , and 3-h dry treatments. Dashed lines indicate the 95% confidence limits.

treatment replicates. Randomization resampling was used to evaluate estimates of handling mortality. Approximate lower and upper 95% confidence limits for handling mortality were computed as the 2.5% and 97.5% percentiles of the bootstrap distributions by using the computer program RT (Manly, 1994).

Results

Spiny lobster

Spiny lobster sample sizes by discard category were sublegal (n=84–88) and berried (n=12–16) (Table 1). All spiny lobsters subjected to the 3-h wet treatment were active at the conclusion of the 2-d baitwell holding period. For dry treatments, the number of active spiny lobsters decreased with increasing exposure time, whereas the number of dead lobsters increased with increasing exposure time. All control lobsters were active, indicating no baitwell holding effects.

Handling mortality (dead/total) for the dry treatment ranged from 12% for the 1-h treatment to 70% for the 3-h treatment (Fig. 4) and did not differ between berried and unberried lobsters (P>0.05). Pooled dead and weak lobsters resulted in a handling mortality that ranged from 16% for the 1-h treatment to 77% for the 3-h treatment (Fig. 5).

Slipper lobster

Handling mortalities for slipper lobster were estimated only for the 3-h dry and wet treatments. Mechanical failure of the baitwell recirculating water pumps during the first 3-h paired dry and wet experiments forced us to reduce the baitwell holding time to 1 day. After the baitwell pumps failed, we repeated the 3-h dry treatment with a 1-d holding period, suspending the holding and control traps 3 m below the sea surface from the *Townsend Cromwell*.

Table 1

Spiny and slipper lobster sample sizes by discard category for each treatment. NB = nonberried and sublegal; B = berried.

	Spiny lobster		Slipper lobster	
Treatment	NB	B	NB	B
1 hour dry	84	16	—	—
2 hours dry	88	12	—	
3 hours dry	87	13	87–89	11–13
3 hours wet	88	12	81	19

Slipper lobster sample sizes by discard category (sublegal and berried) for each treatment are shown in Table 1. Most slipper lobsters subjected to the 3-h wet treatment were active at the end of the 1-d holding period. For the 3-h dry treatment, the number of dead lobsters ranged from 14 to 39, and the number of active lobsters ranged from 56 to 83. All control lobsters were active, indicating no baitwell holding effects.

Slipper lobster handling mortalities for the 3-h dry treatment ranged from 14% to 39% with an average estimate of 27% and were unrelated to berried condition (P>0.05). Estimates of handling mortalities with weak and dead lobsters combined ranged from 17% to 44%, with an average of 31%. Handling mortality for the 3-h wet treatment was 1%.

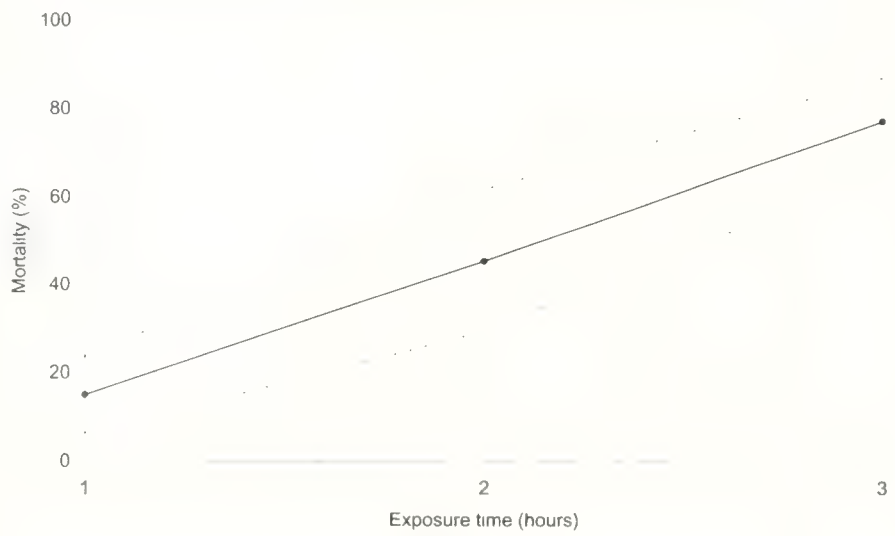

Figure 5

Pooled handling mortality ((dead + weak)/total) estimates for spiny lobster subjected to 1-, 2-, and 3-h dry treatments. Dashed lines indicate the 95% confidence limits.

Discussion

Many factors affect the survival of lobsters discarded in commercial trap fisheries, including capture, handling, and discarding processes. In our experiment we focused on handling factors to assess their impacts on mortality in the NWHI commercial lobster fishery.

If the 2- and 3-h dry experimental treatments typify commercial handling practices, then the mortality of discarded spiny lobster from handling practices on commercial vessels is extreme, ranging from an average of 25% to 45% and 70% to 77%, respectively, depending on how data are pooled. Handling mortality for slipper lobster also appears high (estimated at 31%) but is considerably less than that for spiny lobster; thus spiny lobsters may have a lower handling tolerance than slipper lobsters.

Although there are no published estimates of handling mortality for *P. marginatus* and *S. squammosus*, studies on other lobster species suggest that handling mortality in the NWHI lobster fishery is high. Lyons and Kennedy (1981), reporting on *P. argus*, estimated that 12.3% of lobsters died after 30 minutes of exposure to direct sunlight and an average 24.1% after 1–4 hours of exposures. They also found that lobsters exposed for 2–4 hours tended to die within a week following exposure, whereas those exposed for only 1 hour survived longer. Laboratory experiments by Brown and Caputi (1983) on small western rock lobster, *Panulirus cygnus*, exposed to direct sunlight resulted in an expected time to 50% mortality that decreased with increasing temperature, ranging from 233 minutes at 27°C to 99 minutes at 31–35°C. Time to 50% mortality was 387 minutes for lobsters held in the shade at 26.5–32°C.

Handling mortality, however, represents only a portion of the total mortality of discarded lobsters resulting from their capture, shipboard processing, and subsequent release in the NWHI. Additional mortality resulting from habitat displacement, predation, and other factors associated with discarding might result in total discard mortality estimates that approach 100%. Qualitative evidence suggests that discarded lobsters are subject to high predation from the giant trevally, *Caranx ignobilis*, which aggregate around vessels during fishing operations (Gooding, 1985).

Sorting and discarding lobsters immediately after they are placed on deck appears to reduce total discard mortality. The discarded lobsters would need to be returned to the general vicinity of their capture and as close to the sea floor as possible to avoid the gauntlet of predators in the water column. Brown and Caputi (1986) reported a reduction in recapture rates of displaced undersized rock lobsters compared with nondisplaced rock lobsters and related the reduction directly to predation mortality.

Adoption of the retain-all fishery by the WPRFMC in 1996 significantly reduced fishery-induced handling mortality. Although sporadic discarding occurs, current discard rates are less than 1% and will have no detectable consequence at the population level. The research does, however, provide insight into past fishery-induced handling impacts, which likely contributed to the decline in NWHI lobster catches. If future management again reverted to mandatory discarding practices, this research provides information to assess its impact on fishery-induced mortality. However, to fully understand the synergistic effects of catching, handling, and discarding practices on mortality in the NWHI lobster fishery, additional research to assess the impacts associated with shipboard sorting and releasing (e.g. postrelease predation) is required.

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An evaluation of pop-up satellite tags for estimating postrelease survival of blue marlin (*Makaira nigricans*) from a recreational fishery*

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Blue marlin (*Makaira nigricans*) represent an important commercial and recreational resource throughout tropical and subtropical oceanic waters. In the Atlantic Ocean, blue marlin are managed as a single, oceanwide stock. In the most recent assessment of Atlantic blue marlin (ICCAT, 2001), the Standing Committee for Research and Statistics (SCRS) of the International Commission for the Conservation of Atlantic Tunas (ICCAT) estimated the current biomass of blue marlin to be about 40% of that required for maximum sustainable yield (MSY). Furthermore, the assessment indicated that the current level of fishing mortality (F) was about four times higher than F_{MSY} and that catch levels in recent years were more than twice the equilibrium yield, contributing to a further decline of the overexploited stock. Based on the most recent stock assessment, fishing-induced mortality must be reduced by about 60% to halt the decline of the stock (Goodyear, 2000).

The greatest source of billfish (Istiophoridae) mortality occurs as a result of incidental catches by longline gear deployed for tunas and swordfish (ICCAT, 1997, 2001). These highly migratory species co-occur in the subtropical and tropical epipelagic environment, and all are vulnerable to the pelagic longline. Not all billfish are dead at the time of capture (haulback) on longline gear; data from observers on vessels in the Venezuelan industrial longline fishery indicate that about 49% of blue marlin caught on pelagic longline gear are alive at the time of capture (Jackson and Farber, 1998).

To reduce billfish mortality ICCAT in 1997 required nations to reduce their landings of Atlantic blue marlin by 25% from 1996 levels. Furthermore, the ICCAT SCRS has recommended that the Commission consider requiring the release of all live billfish taken on longline gear (ICCAT, 1997, 2001). It is believed that such a management measure would be more acceptable to member nations than an overall reduction in longline effort that would also reduce catches of target species. However, representatives from several nations have pointed out that there are not sufficient data to estimate postrelease survival of billfish; therefore the conservation impact of a recommendation requiring live released fish cannot be evaluated. In fact, low recovery rates of billfish tagged and released with conventional tags by recreational and commercial fishermen (<2%; Jones and Prince, 1998; Ortiz et al, 1998) are consistent with high postrelease mortality. However, factors such as tag shedding and failure to report tag recaptures could also account for low rates of tag returns (Bayley and Prince, 1994; Jones and Prince, 1998). Clearly, data are needed to support or refute the hypothesis that the release of live billfish would significantly eliminate fishing mortality of blue marlin (Graves et al.[1]).

Acoustic tracking studies designed to investigate billfish physiology and behavior have provided insights into the postrelease survival of billfish taken on recreational gear. Specifically, observed and inferred mortalities during the course of the acoustic tracks indicate that not all released billfish survive (reviewed in Pepperell and Davis, 1999). Unfortunately, it is not possible to estimate levels of postrelease mortality of billfish from previous acoustic tracking studies for several reasons. First, owing to the high cost of ship and personnel time, relatively few animals have been investigated in acoustic tracking studies. Second, because ocean conditions can deteriorate quickly, many of the acoustic tracks were for less than 12 hours duration, providing a limited opportunity to observe mortality after 12 hours. Third, billfish were caught and subsequently tracked under a variety of conditions, making cross-study comparisons difficult. Finally, an estimate of postrelease mortality rates resulting from acoustic studies may be biased because in some cases only healthy fish were selected to carry acoustic transmitters.

The development of pop-up satellite tag technology may present a possible means to estimate postrelease mortality of billfish. Although relatively expensive pop-up satellite tags reduce the need to use a tracking vessel to follow

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billfish on the high seas. Pop-up satellite tags are capable of recording environmental variables over predefined intervals, of detaching from an animal at a designated time, floating to the surface, and of transmitting the stored data to a satellite. Until now, these tags have been deployed primarily on bluefin tuna for relatively long durations (up to nine months) to determine movement patterns (Block et al., 1998a; Lutcavage et al., 1999). Recovery of tag data has been very good in most cases, with some reported rates in excess of 90% (Block et al., 1998a; Lutcavage et al., 1999). These results suggest that the technology may be well suited for shorter term studies, including the determination of postrelease survival. In this paper we present the results of a preliminary study to evaluate the feasibility of applying pop-up satellite tag technology to estimate short-term survival of blue marlin. We also include a brief analysis of the movement and behavior of blue marlin that we inferred from the pop-up tagging results.

Materials and methods

Pop-up satellite tags

The Microwave Telemetry, Inc. PTT-100 pop-up satellite tag was used in this study. The tag can withstand a pressure of 1000 psi (equivalent to a depth of about 650 meters) and is sufficiently small (38 cm by 4 cm diameter) that it would not appear to impose a major drag on a large marine teleost, such as blue marlin (Block et al., 1998a). Tags were programed to measure water temperature every hour and record the mean value for each two-hour period for a total of 61 cycles (122 hours). Inclinometer values were taken every two minutes and summed for the periods before tag detachment (pre-pop-up) and after tag detachment (post-pop-up). For each period the inclinometer started with an initial value of 128. If at the time of measurement (every two minutes) the tag was oriented below 30 degrees above horizontal, a value of one was subtracted from the total. If the tag was above 30 degrees above horizontal at the time of measurement, the inclinometer total was increased by one, but could not exceed 255. Final values below 255 indicated sufficient forward propulsion such that the positively buoyant tag was depressed below 30 degrees above horizontal for certain periods, demonstrating forward propulsion.

All nine tags were programed to detach from the fish 122 hours after activation, at which time the memory within each tag would contain 61 direct temperature measurements and the pre-pop-up inclinometer value. The five-day attachment period of the pop-up tag was chosen, in part, as a result of a review of data from conventional tag-recaptured blue marlin in the Cooperative Tagging Center (CTC) database (E. Prince, unpubl. data). Of the 160 blue marlin tag returns in CTC that have been validated, ten individuals were recaptured within five days of release, suggesting that some blue marlin are able to survive the catching and tagging event and commence feeding again within a few days. In addition, acoustical tagging studies have shown high survival rates of different marlin species in the first 1–2 days following release, demonstrating that mortality, when it occurred, generally happened within the first 48 hours of release (Pepperell and Davis, 1999). With these considerations in mind, we assumed that the five-day period of tag attachment was an adequate period for catch and release mortality to be expressed. As indicated by Goodyear (in press), the duration of this type of experiment should be the minimum number of days necessary to account for postrelease mortality events. Longer periods would allow for greater influence of tag shedding, tag malfunction, and natural mortality, all of which could compromise estimates of postrelease survival.

Tag deployment

Pop-up satellite tags were activated and tested at the start of each fishing day. Blue marlin were caught southwest of Bermuda in the vicinity of Challenger and Argus Banks on standard recreational gear for the blue marlin fishery in Bermuda (130 lb test line) by using trolled high-speed lures or skirted dead baits (in most cases with two hooks). All hooks employed in this study were "J" hooks (no. 16/0–20/0). We tagged the first nine fish available to us. Six blue marlin were caught on the vessels we were aboard. Three individuals were taken on other vessels and transferred to the tagging vessel after the fish were brought to leader (brought to the boat): one blue marlin was caught and attached to a drifting buoy until the tagging vessel, which was several miles away, could gain access to the fish; and two fish were directly transferred after capture from the fishing vessel to the tagging vessel by using a procedure described in Block et al. (1998b).

Once fish were brought to leader (reeled to the side of the boat), quieted and secured, the pop-up satellite tag and a conventional (streamer) tag were deployed. Pop-up satellite tags were attached to one end of a 400-lb (182 kg) test monofilament leader about 18.5 cm in length, with an outside diameter of 1.8 mm. The other end of the leader was attached to a double barb nylon anchor (about 33 mm long and 10 mm wide) made of medical-grade nylon. The anchors were implanted by using a stainless steel tag applicator modified to accomplish placement to a depth of about 10 cm into the dorsal musculature, about 10 cm posterior and 5 cm below the base of the peak of the first dorsal fin (Fig. 1). Hook location, as well as observations on foul-hooking (tissue damage, bleeding, etc.), were noted at the time of hook removal.

Analyses

After detachment from the animal, the positively buoyant tags floated to the surface and began transmitting data to satellites of the Argos™ system. Position information and sections of the temperature and inclinometer data were captured with each satellite pass and transmitted to a ground station and ultimately to the investigators by the internet. Data were analyzed to determine net movement from the point of detachment to the point when the tag popped-up (usually the first tag transmittal; however, if the first satellite pass was near the horizon, the location of the second transmittal was used to obtain greater accu-

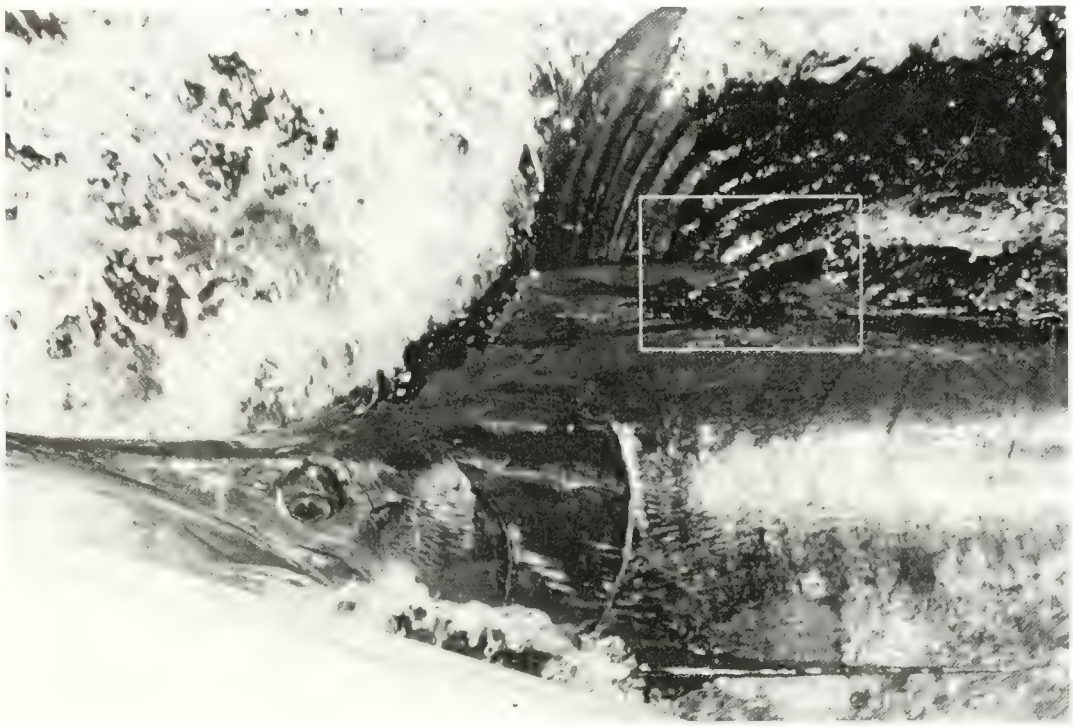

Figure 1

Blue marlin with pop-up satellite tag attached. The tag is located below the anterior portion of the dorsal fin (within outlined area).

racy). Water temperature was determined from temperature sensor readings by using a calibration provided by the manufacturer. Depth was estimated from water temperature values by using temperature and depth relationships provided by the Bermuda Biological Station for Research, which maintains an oceanographic sampling station (station S) about 13 miles (24 km) to the southeast of the island.

Results and discussion

Nine blue marlin, with estimated weights ranging from 150 to 425 lb (68 to 193 kg), were tagged between 25 July and 11 August 1999 (Table 1). Four specimens were below the minimum size for tagging recommended by the tag manufacturer (200 lb or 90.9 kg). Fight times ranged between 15 and 35 minutes. Seven fish were initially hooked in the jaw, and two were "foul-hooked" (i.e. outside the jaw and mouth): one in the operculum and one in the dorsal musculature. After tag placement, but before release, one fish that was originally hooked in the jaw became foul-hooked in the ventral musculature. Three of the nine fish were transferred to the tagging vessel after capture. Fish generally quieted down shortly after being brought to the side of the vessel, which maintained a headway of 4–5 km/h during the tagging operation. Only a few minutes were required to implant the satellite and conventional tags, photograph the fish, estimate weight, measure lower jaw fork length (most individuals), and remove the hook. Condition of the fish varied, and three individuals required resuscitation prior to release.

Eight of the nine tags became detached from their respective host fish after five days, floated to the surface, and transmitted to the Argos™ satellite system. Based on the first accurate location of the tags, net displacements ranged from 40 to 134 nmi (72–248 km) with a mean linear displacement of 90 nmi (167 km) for each individual (Fig. 2). These values are in the range reported for blue marlin by Block et al. (1992) who followed six blue marlin with acoustic transmitters for periods of one to five days. They noted individual total movements (as opposed to net displacements) of 253 km in about three days, 100 km in five days, and four animals with movements of less than 100 km over the course of the respective tracking periods.

Individual marlin in our study dispersed in all directions from their point of release (Fig. 2). The blue marlin tracked by Block et al. (1992) and Holland et al. (1990) in Hawaiian waters moved away from the point of capture in several different directions. However, the authors noted an orientation of movements to the coastline of the Hawaiian Islands. Our releases were farther offshore and an affinity to the Bermuda coastline was not evident from the net movement data.

Depending on the time of tag activation and the time of tag deployment, up to 61 direct water temperature readings, taken every two hours, were obtained for each blue

Table 1

Pop-up satellite tag deployment information. "Transfer" indicates whether a fish was moved between vessels after capture to allow tagging. "Resuscitation" indicates the time spent to move a blue marlin through the water after capture until it could swim off under its own power. Tag no. 24040 failed to report.

Tag no.	Deployment date	Deployment hour	Fight time min.	Transfer (yes/no)	Hook location	Estimated weight (lb)	Resuscitation (no/yes—time)
24519	25 Jul 1999	1610	25	yes	jaw	400	no
24059	28 Jul 1999	1110	35	yes	jaw and ventral musculature	200	no
24522	1 Aug 1999	1030	20	yes	jaw	175	no
24520	2 Aug 1999	1015	15	no	jaw	180	no
24033	2 Aug 1999	1245	30	no	jaw	425	yes–10 min.
24040	2 Aug 1999	1500	17	no	jaw	200	no
24523	3 Aug 1999	1550	15	no	operculum	150	yes–8 min.
24527	11 Aug 1999	1255	15	no	jaw	350	no
24029	11 Aug 1999	1340	23	no	dorsal musculature	150	yes–3 min.

marlin (Fig. 3). Temperature readings demonstrated that tagged individuals spent the majority of their time at temperatures above 26°C (Fig. 4). The maximum temperature range recorded for any of the eight individuals was 9°C (22–31°C, tag no. 24033). Block et al. (1992), using acoustic tracking, determined that the six blue marlin which they tracked spent half of their time in the upper 10 m of the water column in water temperatures 25–27°C, and Holland et al. (1990) reported that blue marlin in waters off Hawaii remained at temperatures of 26° or greater.

Differences in thermal histories were evident among the individuals in our study. Blue marlin no. 24029 (Fig. 3G) spent the vast majority of time at temperatures equal to that of the surface waters (30–31°C). In contrast, individual no. 24527 (Fig. 3H) spent much less time in the warmer surface waters and repeatedly moved up and down in waters between 23° and 31°C. Several individuals appeared to remain at or very near the surface for extended periods, evident in Figure 3 as a continuous string of temperature readings at or slightly above 30°C. An analysis of the data examining diurnal-nocturnal periods with temperature (inferred depth) indicated a high level of variability between individuals and no clear pattern was apparent (Fig. 3). In contrast, Holland et al. (1990) determined that blue marlin spent a higher proportion of their time (~50%) in the upper 10 m at night than during the day (~25%).

It was possible to infer swimming depths of blue marlin by comparing water temperature values with the temperature-depth profiles at station "S" provided by the Bermuda Biological Station for Research.[2] All blue marlin entered cooler waters at various times during the five-day period, with excursions to depths as great as 40 meters. Temperature records were consistent with the tagged blue marlin actively undertaking vertical movements in the upper 40 meters of the water column. However, six of the eight fish spent >75% of their time in the upper 10 m of the water column for the five-day duration of the study. If the data from all eight fish are pooled, this yields a mean value of 79.9% (SD 15.8%) of the time spent in this zone. This is a higher percentage of time spent in the upper 10 m than that observed by Block et al. (1992), who reported that fish spent about half of the time in this zone. However, this comparison should be viewed with some caution because the Block et al. (1992) data were based on continuous tracking, whereas each data point in our analysis was the average of two hourly measurements.

All post-pop-up inclinometer values were 254 or 255, where 255 represented the maximum (vertical) inclinometer value expected for an upright, floating tag. Pre-pop-up inclinometer values ranged from 203 to 251, with three individuals at 233 and four between 247 and 251. These values indicate tags were inclined at an angle below 30 degrees above horizontal for more than 40% of the 1830 sampling times for each individual, and are consistent with sufficient forward propulsion to depress the positively buoyant tag more than 60 degrees from vertical. There was no correlation between pre-pop-up inclinometer values and net displacement. The fish with the largest net displacement (no. 24059) had the second highest inclinometer value. This was not unexpected because the difference between the lowest and highest pre-pop-up inclinometer values represents a minor difference in the time the tag was depressed below 30 degrees above horizontal. Also, the relationship between total movement and net displacement could be quite different for different individuals.

Three different lines of evidence provided by the pop-up satellite tags (net movement, water temperature, and tag inclination) each suggested that at least eight of the

[2] Although this station is situated 24 km to the southeast of the island, similar temperature-depth profiles would be expected for the general region (Johnson, R. 2000. Personal commun. Bermuda Biological Station for Research, 17 Biological Lane, Ferry Reach, St. George's GE01 Bermuda). This allowed us to use the station S profiles to infer swimming depth, realizing that, depending on when an animal was tagged and where it moved, there would be some differences for which we could not account.

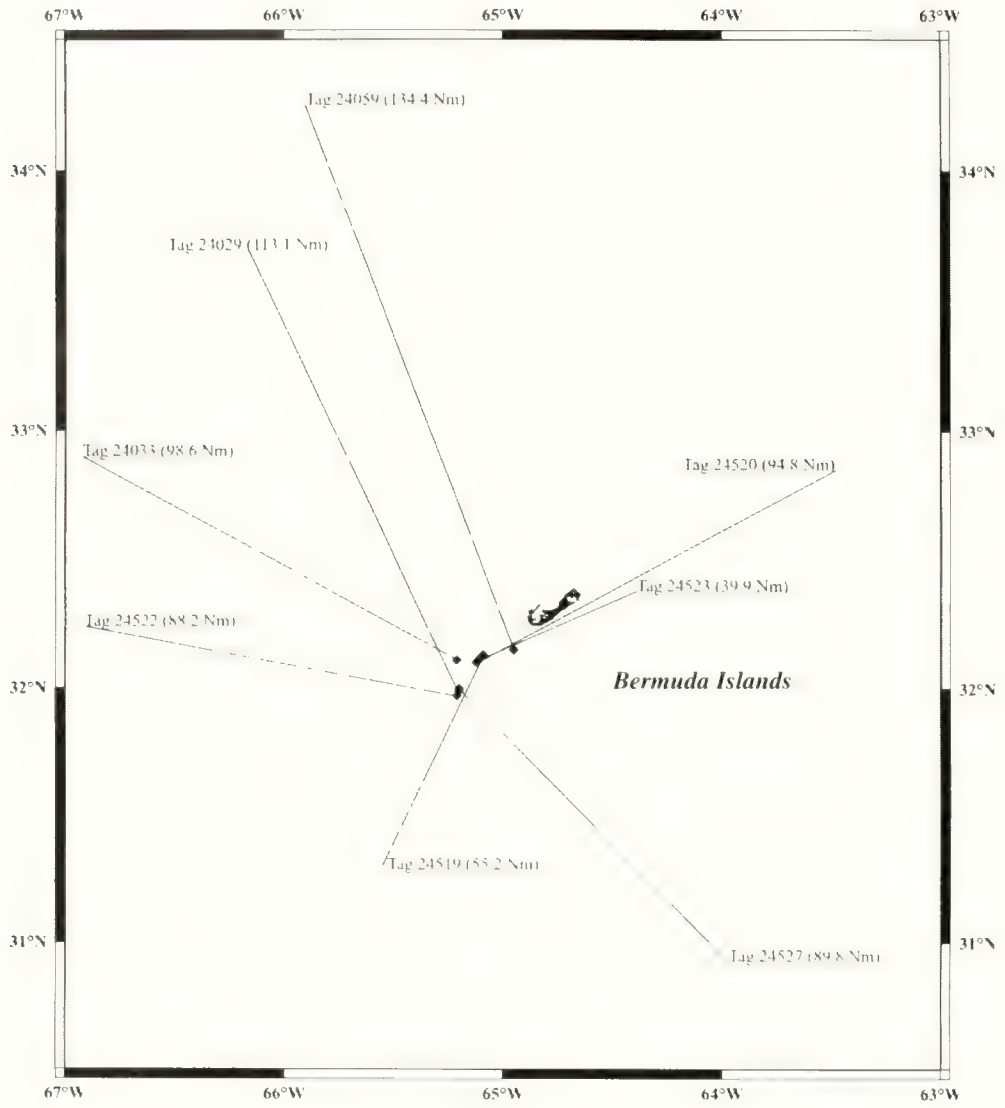

Figure 2

Map showing points of release (squares) and points of recovery (end of straight lines) for eight of nine blue marlin equipped with pop-up satellite tags near Bermuda, 25 July–11 August 1999. The pop-up satellite tag number for each fish and straight line distance between point of release and geolocation where tag transmitted data to the Argos satellite (given in parentheses) are provided.

nine blue marlin caught on recreational gear survived for five days following capture, tagging, and release events. The net movement data indicated a broad dispersal of the eight fish in different directions that cannot be explained by local currents. In contrast to the differing direction of movement, the net displacements of the eight fish were fairly similar. The mean displacement of 89.25 nmi over a five-day period, compares favorably with blue marlin swimming velocities of 1–2 nmi/h reported from acoustic tracking studies (Holland et al., 1990) and is consistent with the constant slow swimming of the individuals. Although currents could have accounted for some of the net displacement, inclinometer values indicated that all eight individuals were actively swimming.

The water temperature measurements indicated that each blue marlin actively undertook dives into cooler water throughout the course of the five days. All eight individuals spent the vast majority of their time in waters with temperatures of 26°C or greater, and no readings below 22°C were recorded.

The successful data recording, tag detachment, and transmission of eight of the nine pop-up satellite tags begs the question of what happened to the one tag that failed to report. It is not possible to distinguish between the postrelease mortality of a tagged blue marlin and the mechanical failure of a pop-up satellite tag. If a marlin dies and sinks in deep water, the attached pop-up satellite tag eventually will be crushed by increasing hydrostatic pressure.

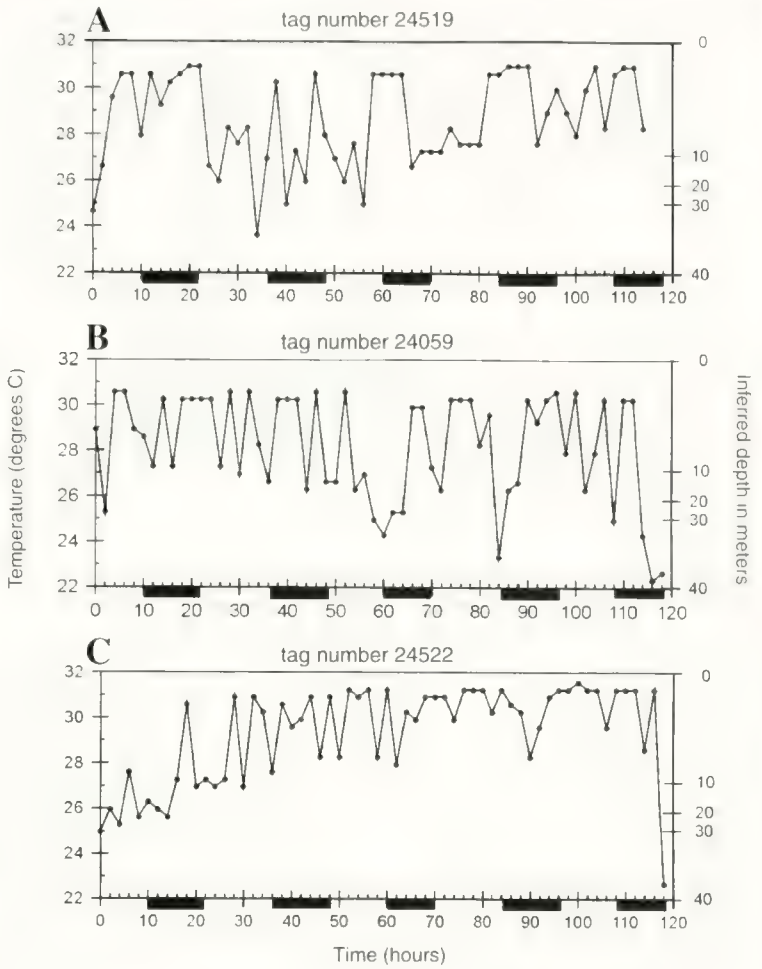

Figure 3

Temperature and inferred depth for eight of nine blue marlin equipped with pop-up satellite tags near Bermuda, 25 July–11 August 1999. See text for explanation of inferred depth and Table 1 for release information corresponding to each tag number. Hours of darkness are shaded on the time line.

The blue marlin whose tag did not report (tag no. 24040, Table 1) was hooked in the jaw, caught in less than 20 minutes, did not require resuscitation, was quickly tagged, and actively swam away from the boat when released. Shark predation on released billfish has been reported (Holland et al., 1990; Pepperell and Davis, 1999); therefore mortality cannot be excluded despite the apparent vigorous condition of the fish. Failures in component subsystems could account for the failure of reporting from a pop-up tag. A detailed analysis of the reliability of each tag component could be undertaken, but several factors external to the tag could also result in a failure of reporting. Tag manufacturer innovations and upgrades of the systems will allow researchers to better identify mortalities, but they will not completely solve the problem of discriminating between tag failure and fish mortality. Nonreporting tags would have significant consequences for efforts to make ocean-wide estimates of postrelease survival. The ability to account for all pop-up satellite tags deployed is directly related to the accuracy of the resulting estimates of postrelease survival (Goodyear, in press). Nonreporting satellite tags introduce uncertainty that cannot be quantified in the estimates of postrelease survival, thus compromising meaningful conclusions. Excluding nonreporting tags from the analysis decreases precision of the estimate, and including mortalities biases the survival estimate downward. Further, any extension of the 5-day pop-up period to allow study of possible delayed effects of tagging should involve careful consideration of the benefits and the liabilities that longer durations might have on estimating postrelease survival (Goodyear, in press)

Successful tagging and reporting of pop-up tags from four fish under 200 lb (90.9 kg) indicate that the size and design of the PTT-100 tag is tolerated by smaller blue mar-

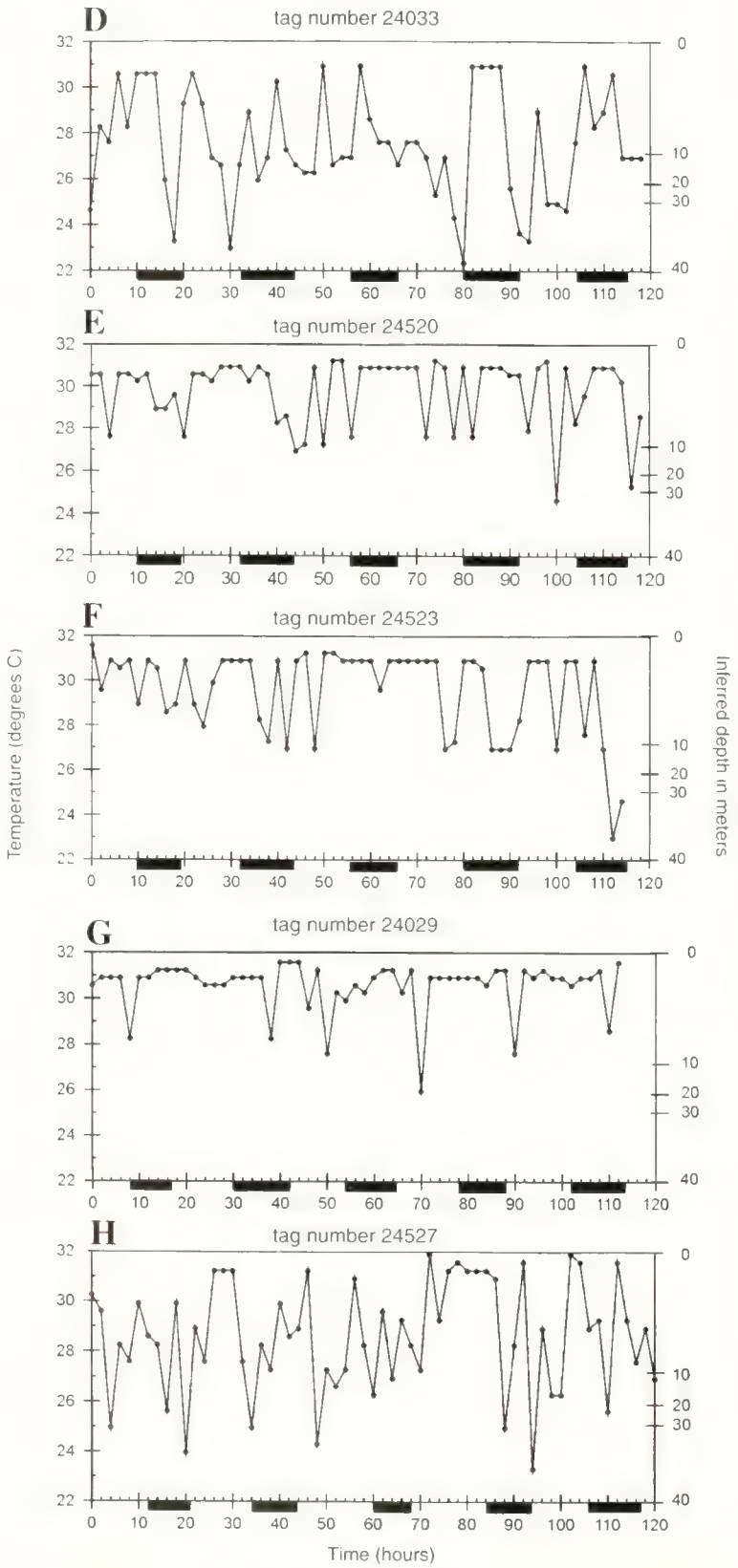

Figure 3 (continued)

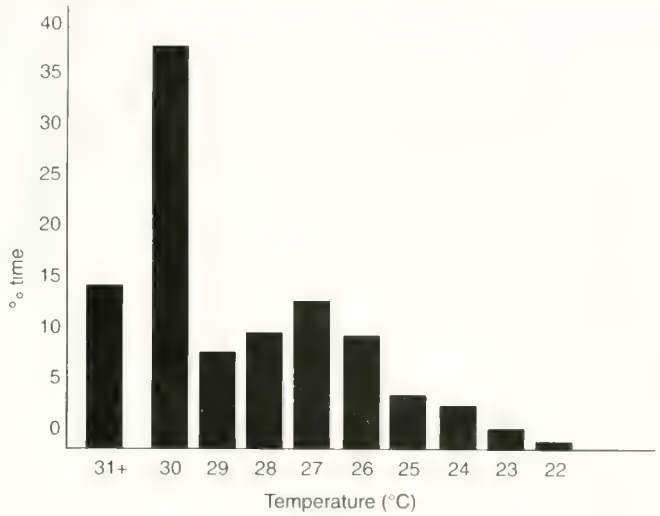

Figure 4

Distribution of time at temperature for eight of nine blue marlin equipped with pop-up satellite tags near Bermuda, 25 July–11 August 1999. Histogram represents combined data for the five-day period of data transmission for each individual.

lin than that recommended by the manufacturer, at least in the short term. Thus a pop-up tag of this size might be tested on even smaller specimens or other target species to expand the study of behavior in a wider size range of species than was originally thought possible.

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Reproduction of the blacknose shark (*Carcharhinus acronotus*) in coastal waters off northeastern Brazil

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The blacknose shark, *Carcharhinus acronotus*, is a relatively small carcharinid, typically inhabiting continental shelf areas in the western Atlantic Ocean, from North Carolina throughout the Gulf of Mexico (Bigelow and Schroeder, 1948) and along the South American coast to Rio de Janeiro (Compagno, 1984). The abundance of this shark in nearshore areas throughout its distribution makes it accessible to commercial fishing, mainly from inshore hook-and-line and gill-net fisheries (Trent et al., 1997; Mattos and Hazin[1]).

Aspects of the biology of *C. acronotus* have been reported by Springer (1938); Bigelow and Schroeder (1948); Clark and von Schmidt (1965); Dodrill (1977); Branstetter (1981); Schwartz (1984); Castro (1993); and Carlson et al. (1999). Schwartz (1984) provided the most comprehensive synopsis, including information on their reproduction and life cycle off North Carolina. Many of the other studies were based on relatively few specimens collected off the southeastern United States and corroborate much of Schwartz's (1984) work, including patterns in spatial and temporal abundances, size at maturity, fecundity, and time of parturition. However, some inconsistencies exist with respect to the duration of the ovarian, gestation, and breeding cycles: i.e. Dodrill (1977) proposed a biennial breeding cycle with gestation taking between 10 and 11 months, Schwartz (1984) suggested a gestation of approximately 9 months, and Branstetter (1981) observed two gravid females with large ovarian eggs (having concurrent ovarian and gestation cycles, copulation having occurred shortly after parturition).

Because *C. acronotus* are represented in catches from various inshore fisheries and carcharhinids typically are characterized by low rates of population increase, adequate information about their reproductive cycle is required to facilitate management of stocks. Given the uncertainty of knowledge about reproduction in *C. acronotus* and the lack of information for the southern part of their range, our aims in the present study were to provide a preliminary overview of the reproductive biology and life cycle of the blacknose shark in coastal waters off northeastern Brazil, using available fishery-dependent data.

Material and methods

Fishing gear used and data collected

Carcharhinus acronotus (79 females and 45 males) were collected from the catches of commercial gillnetters and vessels using bottom longlines off the coast of northeastern Brazil (approx. 7°30′ to 9°30′S—near Recife) between August 1994 and January 1999. The configuration of fishing gears used remained similar over this period. Gill nets were monofilament, 900 m in length, and had a stretched mesh size of 17 cm and a depth of 70 meshes. Nets were set perpendicular to the beach at depths between 5 and 10 m. Bottom longlines consisted of a multifilament mainline (6 mm in diameter) with up to 100 secondary lines, each approx. 5 m in length and constructed from 3-mm diameter monofilament attached to a wire snood (1 m in length). Types of hooks varied among brands, but relative sizes (i.e. 9/0) remained similar. The main baits were sardine (*Sardinella brasiliensis*) and mackerel (*Scomber* spp.), although some other species, including sting ray (*Aetobarus narinari*) and skipjack tuna (*Katsuwonus pelamis*) were occasionally used. Longlines were set on the continental shelf at depths between 10 and 60 m, but most sets were shallower than 40 m. All fishing gears were set at dusk and hauled the following morning at dawn.

All specimens were measured (total length [TL] in the natural position) and dissected. Reproductive organs were removed and stored in a solution of 10% formalin in seawater prior to being transported to the laboratory. Data collected from females included weight and width of the oviducal gland and the functional right ovary, maximum ovarian follicle diameter (MOFD), width of the largest uterus, and, if present, the TL, sex, and number of embryos. Using the methods described by Pratt (1993), we examined the oviducal glands of 10 mature females for the presence of spermatozoa. Length and calcification stage of claspers, width of epididymides, and the presence of seminal fluid in the ampullae of the ductus deferens were recorded from males. Reproductive organs were measured to the nearest 0.1 mm with vernier calipers.

Inferences on stages of reproduction were made according to definitions provided in previous studies on carcharinids (e.g. Pratt, 1979; Hazin et al., 2000). Females were categorized into six stages, mainly based on develop-

[1] Mattos, S. M. G. and F. H. V. Hazin. 1997. Analise de viabilidade economica da pesca de tubarões no litoral do estado de Pernambuco. Boletim Técnico-científico do Cepene, 5: 89–114. IBAMA (Instituto Brasiliero de Meio Ambiente e dos Recursos Naturais Renováveis), Rua Samuel Hardman, s/n Tamandaré – PE, Brazil.

Manuscript accepted 5 July 2001]
Fish. Bull. 100:143–148 (2002).

ment of the oviducal gland, ovary, and uterus. Specimens were considered juvenile if they had undeveloped sexual organs, filiform uteri, and no vitellogenic activity in their ovaries. Pre-ovulatory females had relatively larger ovaries with orange vitellogenic follicles, but no uterine eggs. Ovulating females had uterine eggs and ripe ova still in the ovary, whereas in gravid specimens ovulation was complete. Postpartum females showed similar-size ovaries, oviducal glands, and ovarian follicles as those of gravid specimens, but had flaccid uteri that were still slightly enlarged (compared with other nongravid females) indicating recent parturition. Individuals that had similar-size uteri as those of pre-ovulatory and ovulating individuals, but smaller ovarian follicles with little or no vitellogenic activity were termed "resting" females. Male maturation was evaluated according to development of the testes and claspers. Individuals with relatively short, flexible claspers, and filiform ampullae of the ductus deferens were considered juveniles. Adults were characterized by elongate and calcified claspers and relatively large epididymides (compared with juveniles).

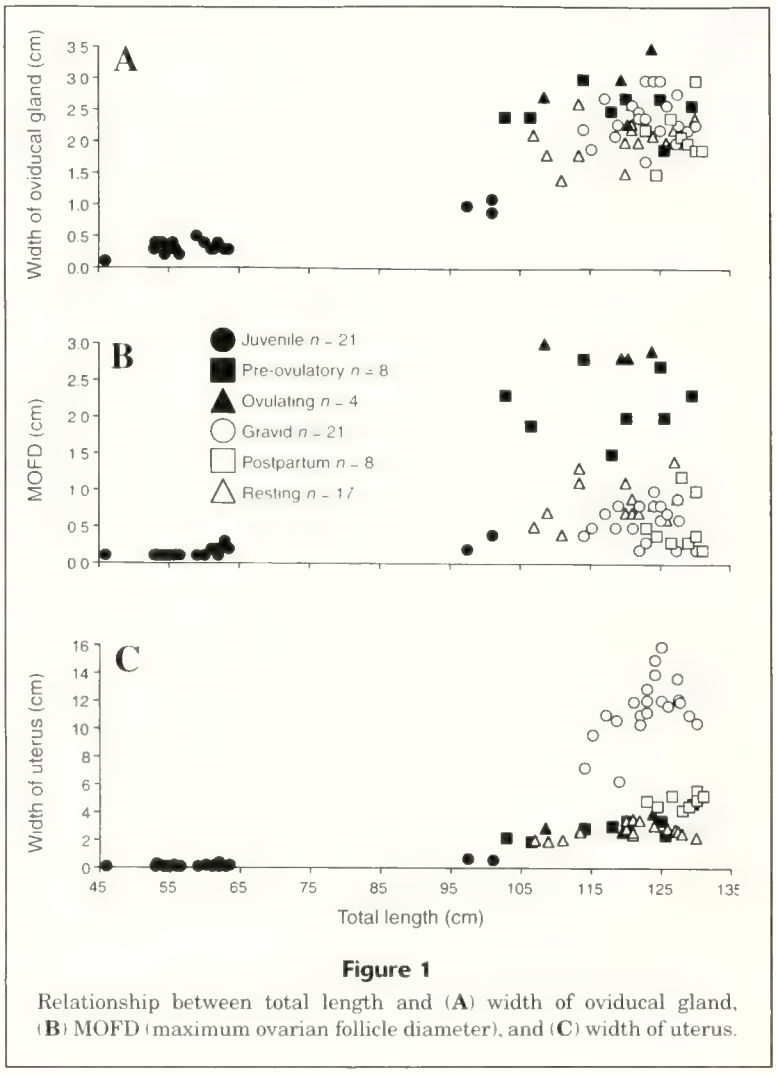

Figure 1

Relationship between total length and (**A**) width of oviducal gland, (**B**) MOFD (maximum ovarian follicle diameter), and (**C**) width of uterus.

Statistical analyses

Size-frequency distributions of males and females were compared by using a two-sample Kolmogorov-Smirnov test (P=0.05). Chi-squared goodness-of-fit tests were used to examine the hypothesis of an equal sex ratio between numbers of juvenile and adult *C. acronotus* sampled and among embryos in gravid females. To help define time of parturition, analysis of variance (ANOVA) was used to investigate the hypothesis of an increase in TL of embryos from near-term females captured in November and December. To provide a balanced analysis, three gravid females captured on 10 December 1998 were analyzed with three individuals captured almost one month earlier on 11 November 1998. Data were assessed for normality by using the Shapiro and Wilk procedure (Zar, 1996), tested for heteroscedasticity with Cochran's test, and then analyzed in the appropriate one-nested factor ANOVA (Underwood, 1981). Gravid females were considered a random-effects factor nested in months and the four embryos for each gravid female were the replicates.

Results

The Kolmogorov-Smirnov test detected significant differences in size-frequency compositions between males and females; proportionally more larger-size females (121–131 cm TL) were captured. Both sexes showed two distinct cohorts. The first consisted of juveniles (46–65 cm) captured by gill nets at depths between 5 and 10 m, and the second included larger specimens (i.e. 85–131 cm), and mostly adults, captured on bottom longlines in deeper water (10 to 60 m). The ratio of juvenile males to females was not significantly different from 1:1 (χ^2=0.027, P>0.01), whereas significantly fewer adult males than females were sampled (ratio of 1:2.34) (χ^2=14.08, P<0.01).

Female maturation and reproduction

Juveniles ranged in size from 46 to 101 cm TL and had narrow oviducal glands, light ovaries with undeveloped white follicles, and thin uteri (Fig. 1, A–C, Table 1). Pre-ovulatory specimens ranged in size from 103 to 129.5 cm TL, had well-developed oviducal glands (width of between 1.9 and 3 cm), and mature ovaries with thick orange follicles (1.5 to 2.8 cm in diameter) (Fig. 1, A and B, Table 1). The shortest pre-ovulatory specimens (e.g. 103 and 106 cm TL), had oviducal glands that were substantially wider (i.e. >2×) than those in the longest juveniles (101 cm TL) (Fig. 1A, Table 1); therefore sexual maturity probably was approached within this size range. This should be con-

Table 1

Characteristics of female *C. acronotus* in each maturation stage and the total length (TL) range and number of specimens. All widths and lengths are in cm, weights in g. MOFD = maximum ovarian follicle diameter.

Characteristic	Juvenile	Pre-ovulatory	Ovulating	Gravid	Postpartum	Resting
Width of oviducal gland	<1.1	1.9–3.0	2.3–3.5	1.7–3.0	1.5–3.0	1.4–2.6
Weight of oviducal gland	2.2–3.0	5.7–8.7	8.6–10.0	2.3–5.0	3.0–5.0	3.0–7.7
Width of uterus	<0.7	1.9–4.7	2.6–3.9	6.3–16	4.2–5.6	1.9–3.5
MOFD	0.1–0.4	1.5–2.8	2.8–3.0	0.2–1.0	0.2–1.2	0.4–1.4
Width of ovary	0.4–1.7	2.3–6.0	4.9–5.7	1.5–3.8	2.2–3.5	1.7–4.0
Weight of ovary	2.7–4.6	12.2–18.2	20.0–24.6	4.5–16.5	12.0–23.0	4.97–16.5
TL of specimens	46.0–101.0	103.0–129.5	108.5–123.8	114.0–130.0	123.0–131.0	107.0–130.0
Number of specimens	21	8	4	21	8	17

sidered a preliminary estimate of size at sexual maturity because few individuals were caught between 95 and 105 cm TL and none between 75 and 95 cm TL. Compared with pre-ovulatory females, those in the process of ovulation had slightly wider oviducal glands and heavier ovaries with thicker follicles (2.8–3 cm in diameter) (Fig. 1, A and B, Table 1). Ovulation appeared to occur only when MOFD was at least 2.8 cm (Fig 1B). The majority of gravid, postpartum, and resting females ranged in size from 111 to 131 cm TL and had similar-size oviducal glands (Fig. 1A, Table 1). Gravid females had undeveloped ovaries with no vitellogenic activity (MOFD was less than 1 cm). Uteri in postpartum females were flaccid and slightly distended (4.2–5.6 cm in width), whereas uteri of resting females were comparable to pre-ovulatory and ovulating individuals (Fig. 1C, Table 1). No mating scars were observed on any of the females. There was no evidence of spermatozoa stored in the oviducal glands of 10 females examined.

The temporal abundance of females according to stages of reproduction showed that juveniles were present in catches between January and November, but mainly from February to June (Fig. 2A). Pre-ovulatory and ovulating individuals were sampled between February and April and April and May, respectively (Fig. 2A). Except for one gravid female caught during August, all gravid, postpartum, and resting females were caught between November and January (Fig. 2A). MOFD of mature females was lowest in August and between November and January, after which it steadily increased to May (Fig. 2B).

Examination of the uterine contents of the 22 gravid females (Table 2) revealed that individual litter size was always four with both sexes present in varying proportions, although the total pooled ratio of males to females (1:1.25) was not significantly different from 1:1 (χ^2=1.13, P>0.05). All embryos from individual gravid females were at similar stages of development and showed small variation in TL. ANOVA detected significant differences in mean TLs of embryos among near-term females (F=20.51, P<0.01) and for the main effect of months (F=10.45, P<0.05). ANOVA showed that the mean (±SE) TL of embryos in three near-term females caught on 10 December 1998 (45.96 ±0.38 cm) was significantly longer than in three near-term females caught on 11 November 1998 (42.31 ±0.07 cm), suggesting that embryos continued to develop between these periods.

Table 2

Date of capture and total length (TL) of gravid *C. acronotus* and the mean TL (±E) and sex ratio of embryos.

		Embryos	
Date of capture	TL of gravid specimen	Mean TL (±SE)	Males: females
17 Aug 94	118.6	29.15 (1.23)	1:3
11 Nov 98	121	42.50 (0.14)	1:3
11 Nov 98	122	45.32 (0.60)	2:2
11 Nov 98	123	40.75 (0.25)	3:1
11 Nov 98	125	43.25 (0.43)	3:1
11 Nov 98	129	45.12 (0.43)	3:1
13 Nov 98	130	38.50 (2.06)	2:2
17 Nov 98	114	34.27 (0.19)	3:1
17 Nov 98	127.7	42.50 (0.15)	3:1
21 Nov 98	115.2	41.37 (0.37)	3:1
22 Nov 98	127.2	45.47 (0.62)	2:2
25 Nov 98	126	43.87 (2.01)	2:2
25 Nov 98	127.5	46.07 (0.22)	1:3
6 Dec 98	117	44.75 (0.14)	2:2
6 Dec 98	123	43.37 (0.85)	2:2
6 Dec 98	123	48.50 (0.28)	2:2
7 Dec 98	125	46.87 (0.12)	2:2
10 Dec 98	124	45.62 (0.37)	2:2
10 Dec 98	124	47.50 (0.28)	3:1
10 Dec 98	122	44.75 (0.25)	2:2
12 Dec 98	123	42.50 (0.35)	3:1
5 Jan 95	114.5	45.37 (0.24)	2:2

Male maturation and reproduction

Of the 45 males examined, 23 were juvenile with thin epididymides (Fig. 3A) and filiform ampullae of the ductus deferens without seminal fluid. Juveniles ranging from 49

to 63 cm TL had relatively short flexible claspers (Fig. 3B) and testes that were not fully differentiated from the epigonal organ. No males between 64 and 87 cm TL were caught. Three juveniles (88, 93, and 94 cm TL) had claspers that were enlarged and beginning to calcify (Fig. 3B) and two larger specimens also had thick epididymides (Fig. 3A). Males appear to approach sexual maturity before 104 cm TL because all specimens longer than this had completely developed sexual organs, including elongate and calcified claspers, thick epididymides, and circumvoluted ampullae of the ductus deferens (Fig. 3).

Discussion

Prevalence of adult females in catches was similar to that from observations made by Schwartz (1984) for stocks off the southeastern United States and can be attributed to a reproductive migration involving relatively large numbers of gravid individuals (114 to 130 cm TL) into the sampled area. Because there was no evidence of disequilibrium between sexes (i.e. there were equal numbers of male and female embryos and juveniles), large numbers of adult males were probably segregated. It is unlikely males were in the sampled area and not caught because females, although proportionally larger, were captured across the same size range (Fig. 1), implying that the selectivity of the gear encompassed the range of sizes of males.

Evaluation of the maturation stages of males and females showed delineation between juveniles and adults. All females longer than 103 cm TL had enlarged oviducal glands and developed ovaries (Fig. 1, A and B, Table 1), and males longer than 104 cm TL had elongate and calcified claspers and thick epididymides (Fig. 3), indicating that sexual maturity was probably approached at these lengths. Although these estimates were derived from few individuals, they are comparable to those proposed by most researchers for specimens collected off the southeastern United States (e.g. Springer, 1938; Clark and von Schmidt, 1965; Compagno, 1984), with the exceptions of Branstetter (1981) who suggested 110 cm TL for both sexes and Schwartz (1984) who suggested 110 cm TL for males.

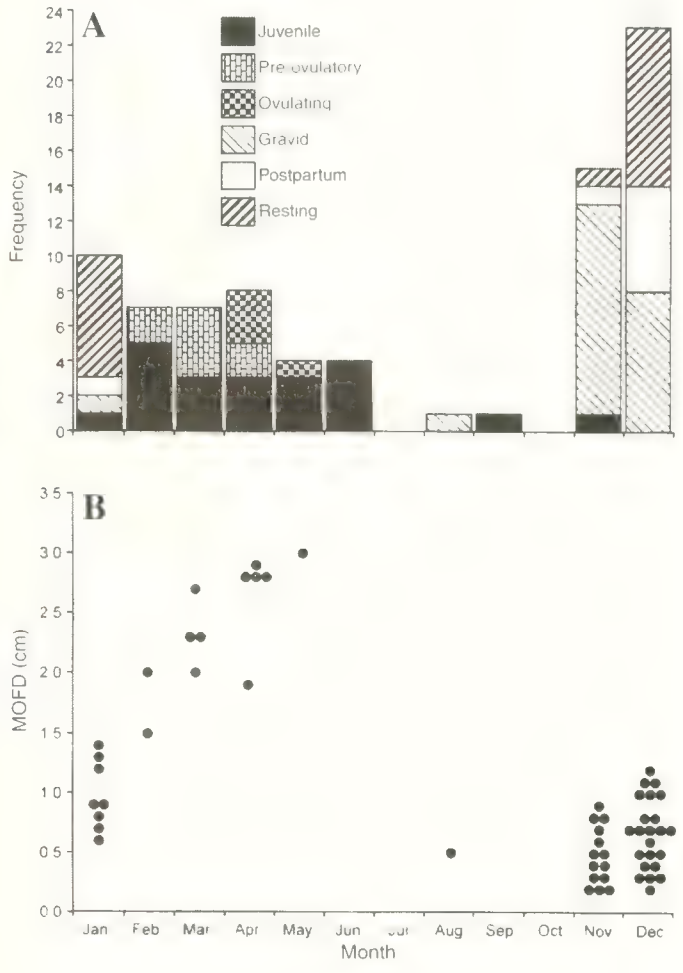

Figure 2

Monthly distribution of (**A**) females in catches according to their stage of reproduction and (**B**) MOFDs (maximum ovarian follicle diameters) for mature females.

Size at birth, number of embryos, sex ratio of embryos, and the time of parturition of *C. acronotus* in our study are consistent with corresponding data from earlier works (Springer, 1938; Clark and von Schmidt, 1964; Dodrill (1977); Branstetter, 1981; Compagno, 1984; Schwartz, 1984). Size at birth has been suggested to be between 45 and 50 cm TL (e.g. Branstetter, 1981; Castro, 1993) and litter sizes commonly range from 3 to 6 (Springer, 1938; Dodrill, 1977; Compagno, 1984). We observed gravid females caught in November and December (late spring to early summer) with embryos longer than 45 cm TL (Table 2). Given the significant increase in size of embryos between these months (indicating that embryos were still developing) and the capture of several neonates (46–51 cm TL) in February and March (late summer to early autumn), we conclude that parturition off northeastern Brazil probably occurs from December to January (mid to late summer). A similar seasonal timing has been proposed for stocks off the southeastern United States (e.g. during June—Schwartz, 1984) and is generally typical for the majority of carcharhinids (e.g. Castro, 1993).

In contrast to the inference made by Branstetter (1981) but in agreement with observations of Schwartz (1984), we showed that vitellogenisis and gestation occur consecutively in *C. acronotus*. Ovaries of adult females off northeastern Brazil begin to mature (pre-ovulatory stage) in February (late summer) with ovulation occurring two to three months later (Fig. 2, A and B). This sequence of events is illustrated by a rapid increase in MOFD from February (1.5–2 cm in diameter) to May (3 cm in diameter) (Fig. 2B). Given the proposed summer parturition (December to Janu-

ary), mating and fertilization during April and May (autumn) would result in a gestation period of approximately 8 months—slightly shorter than that suggested by Schwartz (1984) and Dodrill (1977) (9 and 10 to 11 months, respectively) for stocks off the southeastern United States. Further, the periods required for vitellogenisis and gestation indicate that reproduction of *C. acronotus* off northeastern Brazil could be completed within 10 to 11 months.

With the simultaneous capture of nongravid and gravid females off Florida, Dodrill (1977) proposed a biennial reproductive cycle for *C. acronotus*. Although we also collected gravid and nongravid (i.e. postpartum and resting) females together (i.e. mostly during December and January), the latter individuals could have given birth 3 or 4 weeks earlier. If these females subsequently ovulated 2 months later (in April), then reproduction could conceivably be annual. A fast vitellogenic period, combined with clear reproductive progress, is also supportive of a 1-year cycle. An alternative hypothesis that supports biennial reproduction is that the resting females represented some proportion of segregated nongravid females that moved with the relatively large numbers of gravid females into the parturition area. Given the lack of adult females in catches between June and November (winter to late spring), it is likely, however, that they frequent other areas after copulation. Without additional fishery-independent data, it is impossible to determine these locations and whether some proportion of the female population consists of nongravid or resting individuals throughout the year.

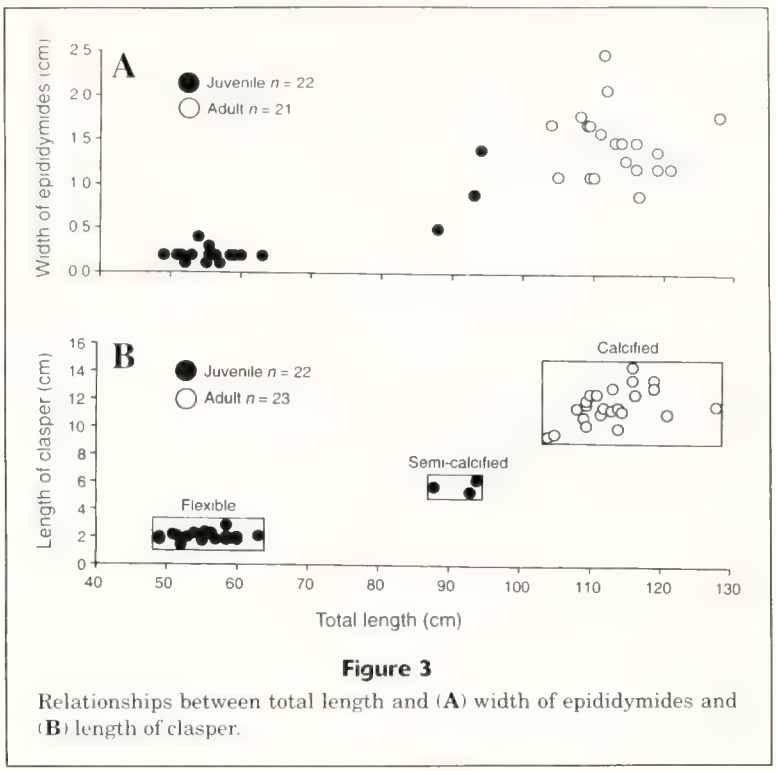

Figure 3

Relationships between total length and (**A**) width of epididymides and (**B**) length of clasper.

Our evidence suggests a shorter reproductive cycle for *C. acronotus* than that previously noted in the literature. Given the 6-month difference between times of ovulation and parturition for females off northeastern Brazil and those off the southeastern United States, our results also indicate the existence of at least two separate stocks. Noting temporal differences in the sizes of embryos from females, Schwartz (1984) proposed two partially separated populations off the southeastern United States: one off North Carolina and the other comprising individuals from Florida and the Gulf of Mexico. Additional research is needed to determine if the population in the southwestern Atlantic is separate from those in the north because the existence of a unit stock off northeastern Brazil would require separate management measures according to the status of that stock.

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A new growth model for red drum (*Sciaenops ocellatus*) that accommodates seasonal and ontogenic changes in growth rates

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The red drum (*Sciaenops ocellatus*) is a popular gamefish found throughout the coastal waters of the Gulf of Mexico and along the eastern seaboard as far north as Massachusetts. Juvenile red drum grow extremely rapidly, especially during the warmer months, but adults grow very little. In fact, the change in growth with age is so abrupt that the standard von Bertalanffy curve has proven inadequate—the predicted lengths of younger fish are generally too large and the predicted lengths of older fish too small (see Beckman et al., 1988; Murphy and Taylor, 1990).

Two generalizations of the von Bertalanffy curve have been found to fit red drum length-at-age data better than the original three-parameter form. The first, dubbed the "double" von Bertalanffy growth curve (Vaughan and Helser, 1990; Condrey et al.[1]), allows the rate at which an animal approaches the asymptotic length to change after some pivotal age, t_p:

$$l_t = \begin{cases} l_\infty\left(1-e^{-k_1(t-t_1)}\right) & \text{if } t < t_p \\ l_\infty\left(1-e^{-k_2(t-t_2)}\right) & \text{if } t > t_p \end{cases} \quad (1)$$

$$t_p = (k_2 t_2 - k_1 t_1)/(k_2 - k_1),$$

where t = age;
l_∞ = asymptotic length;
k_1, k_2 = instantaneous growth rate coefficients; and
t_1, t_2 = age intercept parameters.

The second, dubbed the "linear" von Bertalanffy curve (Hoese et al., 1991; Vaughan, 1996), expresses the asymptotic length as a linear function of age:

$$l_t = (b_0 + b_1 t)(1 - e^{-k(t-t_0)}). \quad (2)$$

Of course other generalizations of the von Bertalanffy curve may also be appropriate, such as the Richards (1959) equation

$$l_t = l_\infty(1-\delta e^{-k(t-t_0)})^{\frac{1}{\delta}} \quad \text{where } \delta \neq 0. \quad (3)$$

The double von Bertalanffy curve accommodates the possibility that older, larger fish might grow more slowly in proportion to their length than younger, smaller fish. (The linear von Bertalanffy curve has no biological interpretation.) In reality, one might expect the growth rate in proportion to length to decrease gradually with the age of the fish rather than at some abrupt pivotal point. Moreover, the growth pattern of juvenile red drum seems to have a strong seasonal component (Goodyear[2]). In this paper a new growth equation is developed that explicitly models these two features. The new equation provided a better fit to northern Gulf of Mexico red drum age-length data than any of the above alternatives.

Materials and methods

The model

The growth rate at any given age t is assumed to be in some proportion k to the difference between the expected size at that age (l_t) and the expected maximum (l_∞):

$$\frac{dl_t}{dt} = k(l_\infty - l_t). \quad (4)$$

Further, k is assumed to decline with age and vary with the seasons such that

$$k = k_0 + k_1 e^{-\lambda_1 t} + k_2 e^{-\lambda_2 t}\sin(2\pi(t - t_s)), \quad (5)$$

where λ_1 and λ_2 are damping coefficients and t_s is a shifting parameter for the sine wave valued between 0 and 1. Substituting Equations 5 and 4 and integrating with $l = 0$ when $t = t_0$ gives

[1] Condrey, R., D. W. Beckman and C. A. Wilson. 1988. Management implications of a new growth model for red drum. Appendix D. *In* Louisiana red drum research, J. A. Shepard (ed.), 26 p. U.S. Dept. Commerce Cooperative Agreement NA87-WC-H-06122. Marine Fisheries Initiative (MARFIN) Program. Louisiana Department of Wildlife and Fisheries, Seafood Division, Finfish Section, Baton Rouge, Louisiana 70803-7503.

[2] Goodyear, C. P. 1996. Status of the red drum stocks of the Gulf of Mexico: report for 1996. Rep. MIA 95/96-47, 21 p. Miami Laboratory, Southeast Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, 75 Virginia Beach Dr., Miami, Fl. 33149.

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$$l_t = l_\infty (1 - e^{\beta_0 + \beta_1 \frac{k_1}{\lambda_1}(t - t_c) + \beta_2 \left[\begin{array}{l} e^{\lambda_1 (t - t_0)} \left(\begin{array}{l} 2\pi \cos\{2\pi(t - t_0)\} - \\ \lambda_2 \sin\{2\pi(t - t_0)\} \end{array} \right) \\ e^{\lambda_1 (t_c - t_0)} \left(\begin{array}{l} 2\pi \cos\{2\pi(t_c - t_0)\} \\ \lambda_2 \sin\{2\pi(t_c - t_0)\} \end{array} \right) \end{array} \right]})$$

$$\beta_1 = \frac{k_1}{\lambda_1}(e^{\lambda_1 t} - e^{\lambda_1 t_c})$$

$$\beta_2 = \frac{k_2}{4\pi^2 + (\lambda_2)^2} \left[\begin{array}{l} e^{\lambda_1 t} \left(\begin{array}{l} 2\pi \cos\{2\pi(t - t_0)\} - \\ \lambda_2 \sin\{2\pi(t - t_0)\} \end{array} \right) \\ e^{\lambda_1 t_c} \left(\begin{array}{l} 2\pi \cos\{2\pi(t_c - t_0)\} \\ \lambda_2 \sin\{2\pi(t_c - t_0)\} \end{array} \right) \end{array} \right]. \quad (6)$$

Assuming the animal will not shrink with age, i.e., $dl/dt \geq 0$, implies the constraint

$$k_0 + k_1 e^{\lambda_1 t} + k_2 e^{\lambda_1 t} \sin(2\pi(t - t_c)) \geq 0. \quad (7)$$

Equation 6 may appear formidable, but typically requires only a minute or two more to enter into standard statistical fitting packages. It reduces to a form similar to the Gompertz equation when $k_2 = 0$ and to the von Bertalanffy equation when $k_1 = k_2 = 0$.

Fitting the model to data

Equations 1, 2, 3, and 6 were fitted to observations of length-at-age from red drum collected in the northern Gulf of Mexico between September 1985 and October 1998 (see Beckman et al., 1988, or Wilson et al.[3] for further details regarding the data collection and aging procedures). The fitting was accomplished by ordinary least squares by using a Nelder-Mead simplex search[4] and, as a check, proc NLIN of SAS (1990). The least-squares solution is equivalent to the maximum likelihood solution when the distribution of length at age is normal with constant variance, which seems to be approximately true of this particular data set (Porch, unpubl. data).

Akaike's (1973) information criterion (AIC) was used to rank the growth models in terms of their ability to provide statistically parsimonious explanations of the data. The formula for the AIC may be written

$$AIC = -2\log(L) + 2p,$$

where L is the likelihood function and p is the number of parameters (see Buckland et al., 1997). In this case, $-2\log(L)$ is equal to the residual sums of squares.

Table 1

Akaike's information criteria (AIC) quantifying the fit of the various growth models to the red drum length-at-age data. Smaller AIC values indicate statistically better fits.

Model	Number of parameters	Negative log-likelihood	AIC (−25,000)
von Bertalanffy	3	16045.9	7098
Richards	4	14169.8	3348
linear von Bertalanffy	4	12883.8	776
double von Bertalanffy	5	12876.6	763
damped (Eq. 6, k_2=0)	5	12651.3	313
seasonal + damped (Eq. 6)	8	12584.9	186

The parameter estimates for the Richards equation tended to be unstable unless good initial estimates were provided. This was accomplished by conducting the estimation in two stages. In the first stage the exponent δ was fixed to 1 and the other parameters were estimated, reducing the Richards equation to the von Bertalanffy form. In the second stage the initial guesses were set equal to the final estimates from the first stage and then all four parameters were estimated simultaneously.

Results and discussion

All five alternative growth models fitted the data significantly better than the von Bertalanffy equation according to the AIC statistic (Table 1). The Richards equation, however, did not fit the data nearly as well as the other alternative formulations and suffered from well-known instability problems (Ratkowsky, 1983), therefore it can probably be dropped from any future consideration with respect to red drum. The double von Bertalanffy curve fitted the data better than the linear von Bertalanffy curve, but the comparison is rendered moot by the performance of the new model. The five-parameter version without seasonal oscillations (Eq. 6 with k_2=0) fitted the data significantly better than either. The eight-parameter version with seasonal oscillations fitted the data significantly better still (see Fig. 1).

The estimated seasonal component to the growth rate was fairly substantial initially, having an amplitude at age 0 of 0.301 (k_2) and a peak in June, but declined rapidly with age (Fig. 2). It is possible that an even stronger seasonal signal would have been estimated if age-0 fish, which exhibit the strongest seasonal pattern (Goodyear[4]), had been adequately represented in the sample.

Some of the parameter estimates were highly correlated, as is the case in most growth studies. In particular, the correlations between the estimates for the growth rate and asymptotic length coefficients were typically above 0.8. However, the asymptotic variance-covariance matrix

[3] Wilson, C. A., D. L. Nieland and A. L. Stanley. 1993. Variation of year-class strength and annual reproductive output of red drum *Sciaenops ocellatus* and black drum *Pogonias cromis* from the northern Gulf of Mexico. Final Report 1991–1992, 31 p. U.S. Dept. Commerce Cooperative Agreement NA90AA-H-MF724. Marine Fisheries Initiative (MARFIN) Program. Coastal Fisheries Institute. Louisiana State University, Baton Rouge, La 70803-7503.

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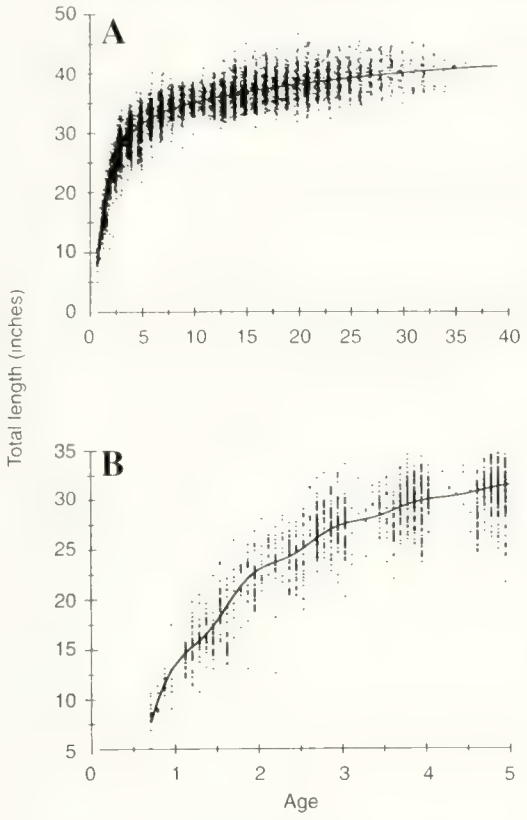

Figure 1

Fit of the proposed seasonal growth model to red drum length at age data: (**A**) the fit for all ages; (**B**) the fit for the younger ages.

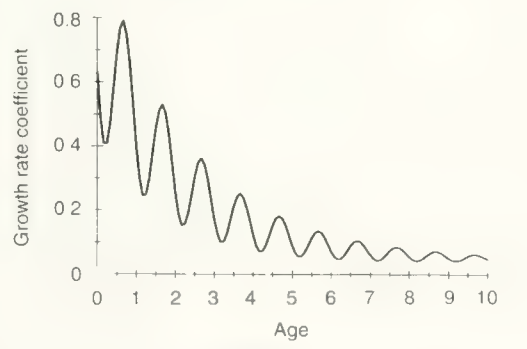

Figure 2

Growth rate coefficient from seasonal model as a function of age.

suggests that the parameters for all of the models were estimated fairly precisely (Table 2).

The new model, either with or without the seasonal component, has both practical and theoretical advantages over the four other models examined in this study. By virtue of its greater flexibility, it was able to fit the red drum data significantly better than the linear and double von Bertalanffy curves (its nearest competitors). Moreover, the Richards and linear von Bertalanffy curves are theoretically disadvantaged because their parameters have no physical interpretation. The double von Bertalanffy curve, although it has a physical interpretation, suffers because it allows only a single discontinuous change in the growth rate at one age rather than a continuous change through time. For these reasons, the new model should be more widely applicable than the others, particularly for species that change habitat preferences with age or are subject to strong seasonal environmental fluctuations.

Table 2

Parameter estimates and corresponding coefficients of variation (CV) derived from the asymptotic covariance matrix.

Model	Parameter	Estimate	CV (%)
von Bertalanffy	l_∞	37.7	1
	k	0.323	1
	t_0	–0.646	3
linear von Bertalanffy	b_0	32.5	1
	b_1	0.284	1
	k	0.590	9
	t_0	0.126	1
double von Bertalanffy	l_∞	40.0	1
	k_1	0.412	1
	t_1	0.0530	23
	k_2	0.114	2
	t_2	–8.41	3
damped (Eq. 6, k_2=0)	l_∞	44.1	1
	k_0	0.0416	7
	t_0	0.362	3
	k_1	0.667	2
	λ_1	0.464	1
seasonal and damped	l_∞	43.4	1
	k_0	0.0475	5
	t_0	0.443	3
	k_1	0.695	2
	λ_1	0.476	1
	k_2	0.301	16
	λ_2	0.344	22
	t_c	0.439	3

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Horizontal and vertical movements of juvenile bluefin tuna (*Thunnus thynnus*), in relation to oceanographic conditions of the western North Atlantic, determined with ultrasonic telemetry

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Abstract—We employed ultrasonic transmitters to follow (for up to 48 h) the horizontal and vertical movements of five juvenile (6.8–18.7 kg estimated body mass) bluefin tuna (*Thunnus thynnus*) in the western North Atlantic (off the eastern shore of Virginia). Our objective was to document the fishes' behavior and distribution in relation to oceanographic conditions and thus begin to address issues that currently limit population assessments based on aerial surveys. Estimation of the trends in adult and juvenile Atlantic bluefin tuna abundance by aerial surveys, and other fishery-independent measures, is considered a priority.

Juvenile bluefin tuna spent the majority of their time over the continental shelf in relatively shallow water (generally less then 40 m deep). Fish used the entire water column in spite of relatively steep vertical thermal gradients (≈24°C at the surface and ≈12°C at 40 m depth), but spent the majority of their time (≈90%) above 15 m and in water warmer then 20°C. Mean swimming speeds ranged from 2.8 to 3.3 knots, and total distance covered from 152 to 289 km (82–156 nmi). Because fish generally remained within relatively confined areas, net displacement was only 7.7–52.7 km (4.1–28.4 nmi). Horizontal movements were not correlated with sea surface temperature. We propose that it is unlikely that juvenile bluefin tuna in this area can detect minor horizontal temperature gradients (generally less then 0.5°C/km) because of the steep vertical temperature gradients (up to ≈0.6°C/m) they experience during their regular vertical movements. In contrast, water clarity did appear to influence behavior because the fish remained in the intermediate water mass between the turbid and phytoplankton-rich plume exiting Chesapeake Bay (and similar coastal waters) and the clear oligotrophic water east of the continental shelf.

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Fish. Bull. 100:155–167 (2002).

Current estimates of spawning biomass for Atlantic bluefin tuna (*Thunnus thynnus*) remain controversial (Butterworth and Punt, 1993; Restrepo et al., 1994; Restrepo, 1996), although the most conservative predicts that a population eight times the current size would be needed to produce maximum sustainable yields (Sissenwine et al., 1998). The current strict catch quotas are based on abundance assessments for both adult and juvenile (i.e. "schooling") fish (age classes 1–5 years, body mass ≈6–60 kg). Adult abundance is derived from commercial landings data; juvenile abundance has, since 1985, been based on fishing effort and landings data obtained from dockside intercepts and telephone polling of the largely recreational fishery for juvenile bluefin tuna conducted by the National Marine Fisheries Service's Large Pelagics Survey (Turner et al., 1993, 1997). The usefulness of both data sets can be compromised, however, because the relationship between catch-per-unit-of-effort (CPUE) data and real abundance is not known with certainty (Bakun et al., 1982; Hilborn and Walters, 1992; Lauck, 1996). This problem is especially critical with highly mobile schooling fishes like tunas because of environmental influences on fish distribution and vulnerability to specific fishing gears, as well as the introduction of new fishing techniques (Sharp, 1978; Clark and Mangel, 1979; Brill, 1994; Bertrand and Josse, 2000).

Juvenile Atlantic bluefin tuna appear in the surface waters off the east coast

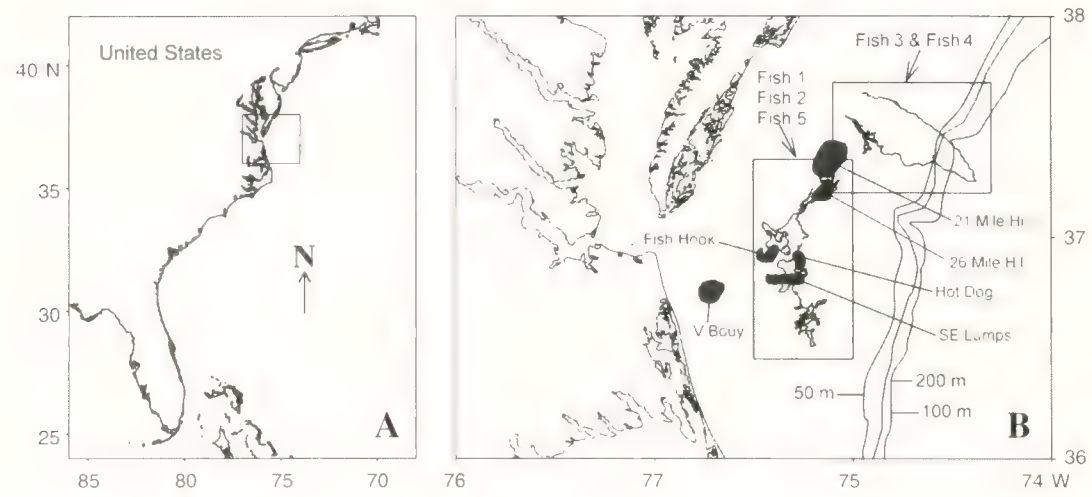

Figure 1

(**A**) Map of the east coast of the United States. The rectangle shows the area enlarged in panel B. (**B**) Movements of five juvenile bluefin tuna (*Thunnus thynnus*). The limit of the continental shelf is shown by the 50-, 100-, and 200-m isobath lines. The topographic features considered by local fishermen to aggregate juvenile bluefin tuna are shown by the shaded areas. Place names are taken from local fishing charts. The rectangles show the areas enlarged in Figures 3 and 4.

of the United States, from North Carolina to Rhode Island, usually during June and July (Rivas, 1978; Sakagawa, 1975; Roffer, 1987; Lucy et al., 1990; Mather et al., 1995). Their presence provides an opportunity for direct population assessments with aerial surveys similar to those conducted on adult Atlantic bluefin tuna (Lutcavage and Kraus, 1995; Lutcavage et al., 1997), southern bluefin tuna (*Thunnus maccoyii*),[1] and other fish species (e.g. Lo et al., 1992). Assessments of juvenile bluefin tuna abundance are considered particularly crucial for effective stock management because these will allow the forecasting of recruitment and long-term population trends (Polacheck et al., 1996; Sissenwine et al., 1998). There is, however, a need to establish the probability of detecting schools and estimating school size before aerial survey data can provide robust population assessments. This need is present regardless of whether the census techniques are simple photography (Lutcavage and Kraus, 1995; Lutcavage et al., 1997) or new laser-based digital remote sensing techniques (Oliver et al., 1994; Lo et al., 1999). As with traditional CPUE-based abundance estimates, knowledge of the effects of oceanographic conditions on depth distribution, surfacing frequency, travel speeds, and residence patterns is critical because these conditions will affect vulnerability to "capture," either on photographic film or as digital data.

To obtain the necessary data, we undertook a study of the horizontal and vertical movements of juvenile Atlantic bluefin tuna using depth sensitive ultrasonic telemetry devices. Ultrasonic telemetry is a proven technique for acquiring the required precise and detailed data on the behaviors of pelagic fishes in relation to oceanographic conditions (e.g. Holland et al., 1990; Dagorn et al., 1999, 2000a; Lutcavage et al., 2000). Besides being useful for improving stock assessments (Brill and Lutcavage, 2001), the resultant data can also help clarify basic ecological relationships and provide inferences on physiological abilities and species-specific behaviors (Carey, 1983; Brill, 1994; Brill et al., 1999).

Materials and methods

Fishing operations were conducted from a 16-m commercial fishing boat (FV *Grumpy*) in the western North Atlantic off the eastern shore of Virginia (Fig. 1A) during June and July 1998. Bluefin tuna were captured with standard recreational trolling gear. The fish were brought aboard with a plastic sling and detached from hooks. Straight line fork length was measured, and a Vemco (Halifax, Nova Scotia, Canada) ultrasonic transmitter (model V32) was attached near the second dorsal fin with nylon straps as described by Holland et al. (1986, 1990). The transmitted signal was detected with a Vemco VR-60 ultrasonic receiver connected to a directional hydrophone mounted on the end of an aluminum pipe. The pipe was clamped to the side of the vessel with a custom designed aluminum bracket that allowed the hydrophone to be rotated to find the relative bearing to the transmitter. Fish depth, encoded by the interval of the transmitter's pulsed signal, was decoded by the receiver and the resultant digital data recorded by an attached laptop computer. Geographic

[1] Cowling, A., C. Millar, and T. Polacheck. 1996. Data analysis of the aerial surveys (1991–1997) for juvenile southern bluefin tuna in the Great Australian Bight. Rep. RMWS/96/4, 87 p. Recruitment Monitoring Program, CSIRO Division of Marine Research, GPO Box 1538, Hobart 7001, Australia.

Table 1

Summary of tracks of five juvenile Atlantic bluefin tuna (*Thunnus thynnus*) equipped with ultrasonic depth sensitive transmitters. Body masses were calculated from fork lengths with the weight-length regression equation provided by Coull et al. (1989).

Fish no.	Fork length cm	Body mass kg	Dates of track (1988)	Duration of track h	Total distance covered km (nmi)	Distance between start and end points km (nmi)	Mean (± SEM) swimming speed knots
1	74	6.7	17–19 Jun	47.2	217 (117)	52.7 (28.4)	2.8 ±0.03
2	91	12.1	23–25 Jun	47.8	267 (144)	11.4 (6.1)	3.0 ±0.03
3	79	8.0	2–3 Jul	30.0	152 (82)	7.7 (4.1)	2.7 ±0.04
4	99	15.4	6–7 Jul	31.2	192 (104)	14.7 (7.9)	3.3 ±0.03
5	106	18.8	10–12 Jul	47.9	289 (156)	32.2 (17.4)	3.2 ±0.03

positions were obtained by using a GPS satellite receiver and were recorded on a second laptop computer every minute. The tracking vessel's position was assumed to be the same as that of the fish. Sea surface temperature and bottom depth were recorded manually every 15 minutes by using a hull-mounted electronic temperature sensor and color fathometer, respectively. Depth-temperature profiles were taken approximately every four hours with a Sippican (Marion, MA) portable XBT system (model MK12).

Aggregate time-at-depth and time-at-temperature distributions were calculated from10-m and 1°C bins (respectively), as described by Holland et al. (1990). These data were subsequently expressed as a fraction of the total time each fish was followed, and the fractional data bins were averaged across all fish. Speed over ground (henceforth referred to simply as "speed") was calculated by assuming that the fish moved in a straight line between successive geographic locations.

Sea surface temperature (SST) data were recorded by the advanced very high resolution radiometer (AVHRR) carried onboard the NOAA-14 polar orbiting operational environmental satellite. High resolution picture transmission (HRPT) data were obtained from the National Coast Watch Active Access System at the National Oceanographic Data Center and had a spatial resolution of 1.25 × 1.25 km pixels. Ocean color data were recorded by the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) carried onboard the Orbview-2 spacecraft (Orbimage, Inc., Dulles, VA). The level-2 global area coverage (GAC) data were obtained from the NASA Goddard Space Flight Center's Distributed Active Archive Center. These 4-km resolution data sets included chlorophyll-*a* surface concentration and the diffuse attenuation coefficient at 490 nmi, *in vacuo*. We calculated the occupancy of waters with specific chlorophyll-*a* concentrations and light attenuations from values corresponding to and coincident with the tracks of fishes derived from satellite images. These data were subsequently expressed as a fraction of the total number of observations for each fish, and the fractional data bins were averaged across all fish. For illustrative purposes, we also generated composite images using data from the 21-day period over which all tracking operations were conduced.

Results

The bottom topography in the areas where the fish were tracked is generally featureless, except for small areas where the vertical relief is approximately 2 m above the surroundings. Local fishermen have named these features (Fig.1B and subsequent figures), and the names used in this study are taken from local fishing charts.

Size of fish, starting and ending dates of tracks, duration of tracks, distances covered, distance between starting and ending points, and mean (±SEM) swimming speed of fish are listed in Table 1. With the exception of fish number 4 (referred to simply as "fish 4"), individuals tended to follow highly irregular courses that often repeatedly covered the same areas (Fig. 1B). The mean distance between starting and ending points for all fish was only 11% (range: 4–25%) of the total distance covered (Table 1). From tracking studies of yellowfin tuna (*Thunnus albacares*) in the Pacific, Dagorn et al. (2000a) concluded that such frequent directional changes might be characteristic of foraging behavior. The frequency of observed swimming speeds is shown in Figure 2. Although all fish reached maximum speeds of ≈7 knots for brief periods, over 90% of the observed speeds were less than 3.6 knots.

Horizontal movements

Fish 1 was captured and released at 1340 h, approximately 1.8 km (1 nmi) west of the "26 Mile Hill" (Fig. 3). It proceeded on a southerly course for about 33 h, a direction that carried it over the "Hot Dog" and "Southeast Lumps." After sunset on the second day, the fish reversed its course and eventually recrossed both features. The fish was approximately 5.6 km (3 nmi) south of the "Southeast Lumps," and moving south, when the track was terminated at 1300 h.

Fish 2 was captured approximately 5.6 km (3 nmi) south of the "Southeast Lumps" (Fig. 3) at 1547 h, adjacent to where the track of fish1 was completed four days earlier. It

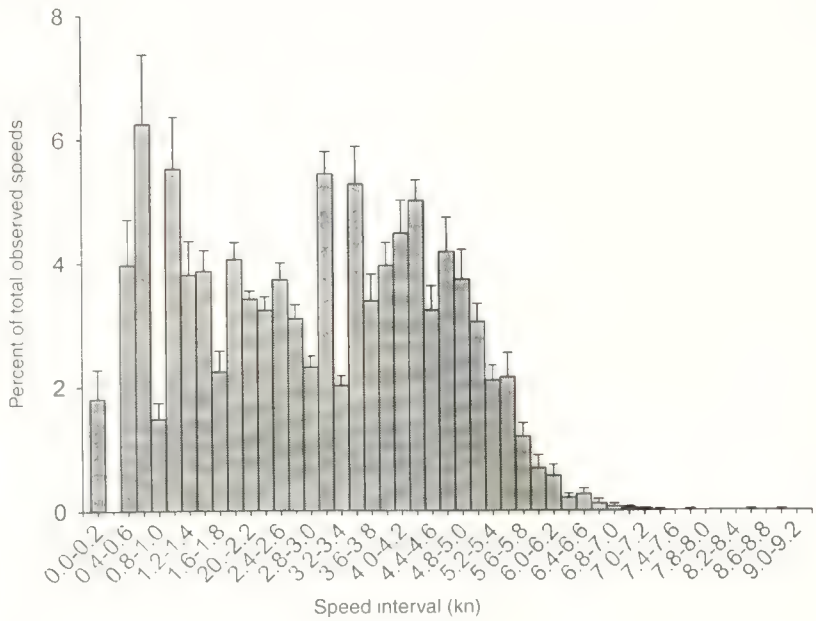

Figure 2

Frequency histogram (mean ±SEM) of observed speed over ground of bluefin tuna. The frequency of each speed interval was calculated as a fraction of the total number of observations for each fish, and speed intervals where then averaged across fish.

proceeded south, then briefly west just before dusk. After dark it turned to the northeast, and then assumed a parallel course to the southwest. From 1000 h on the second day until the end of the track, the fish repeatedly crisscrossed an area approximately 18 km (10 nmi) southeast of the "Southeast Lumps." The fish made one brief excursion during the second day but generally remained in this area until the track was terminated at 1545 h.

Fish 3 was captured and released at 1140 h approximately 11 km (6 nmi) northeast of the "21 Mile Hill" (Fig. 4). It proceeded to the northwest for approximately 4 hours, then turned and retraced its course returning to the point where it was captured approximately 6 hours earlier. This general pattern was repeated for the remainder of the track. Fish 3 favored an area approximately 11 km (6 nmi) northeast of the "21 Mile Hill," although it moved briefly away from this area during the first night and second day.

Fish 4 was captured and released at 1300 h in the same area (northeast of the "21 Mile Hill") as fish 3 (Fig. 4). Its behavior differed significantly from all the other fish in that it swam two relatively straight courses. The first was to the southeast (from the time of release until sunrise the following day) and the second to the northwest (from sunrise until the track ended at 2015 h). (The track had to be abandoned after approximately 31 h when the fish moved into an active U.S. Navy missile test area.) It was also the only individual that moved offshore of the continental shelf.

Fish 5 was captured and released at 1330 h immediately adjacent to the "21 Mile Hill" (Fig. 3). During the first day, the first night, and the morning of the second day the fish stayed either over or adjacent to the "21 Mile Hill" and "26 Mile Hill." It eventually followed a relatively straight course to an area approximately 5.5 km (3 nmi) northeast of the "Fish Hook," were it remained until the track was terminated after 48 hours.

Vertical movements

The vertical movements of the four fish that remained on the continental shelf are shown in Figure 5. Juvenile bluefin tuna made use of the entire water column and undertook frequent, albeit brief, forays to the bottom. Fish 4 showed similar behavior but reached maximum depths of approximately 160 m when its course carried it eastward of the continental shelf (Fig. 6). No abrupt vertical movements were apparent at dawn and dusk, as have been observed in adult Atlantic bluefin tuna (Lutcavage et al., 2000) and juvenile Pacific bluefin tuna (*Thunnus orientalis*) (Marcinek et al., 2001). Similarly, there were no dramatic and unambiguous differences in daytime and nighttime vertical movement patterns (Figs. 5 and 6), as has been observed with bigeye tuna (*Thunnus obesus*) (Holland et al., 1990; Dagorn et al., 1999).

Figure 7 presents the mean (±SEM) time spent at specific depths and at specific temperatures. Juvenile bluefin tuna spent ≈90% of the time at depths less than 15 m, but less than 20% of the time at depths above 3 m. There were no clear differences in daytime and nighttime depth distri-

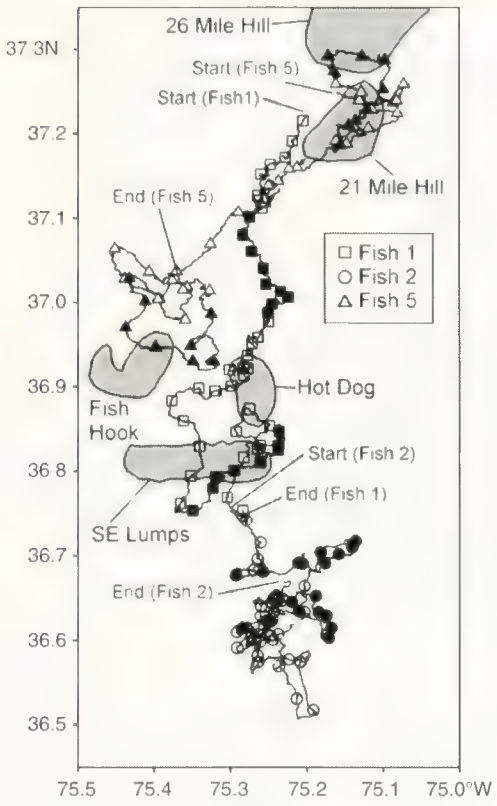

Figure 3

Movements of fish 1, 2, and 5. Symbols represent hourly intervals: open symbols indicate daytime and solid symbols, nighttime.

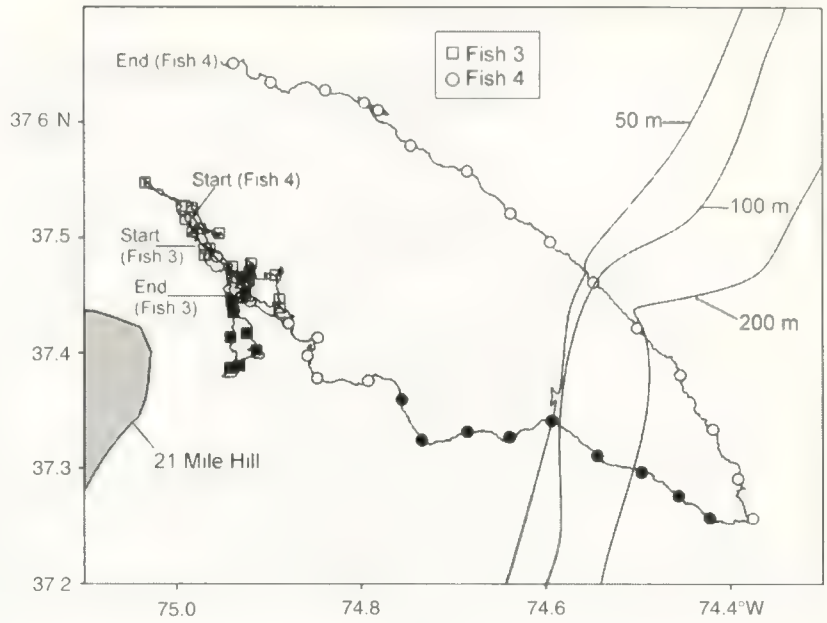

Figure 4

Movements of fish 3 and 4. Symbols represent hourly intervals: open symbols indicate daytime and solid symbols, nighttime. The edge of the continental shelf is shown by the 50, 100-, and 200-m isobath lines.

butions. Although they encountered water temperatures of ≈10°C during their brief descents, fish spent ≈90% of the time in water greater than 20°C and ≈50% of the time in water greater than 24°C.

Occupancy of specific water masses

Figure 8 shows fish movements and sea surface temperatures (SST). Note that specific water masses (except for the Gulf Stream, a portion of which is clearly visible to the southeast) appear ill-defined by SST (Fig. 8). (During the 21-day study period, there was no evidence that an instability in the Gulf Stream resulted in discharge of warm, high-salinity water onto the Virginia continental shelf, as has been occasionally observed [Churchill et al., 1993].)

Figure 9 presents fish movements and chlorophyll-*a* concentrations (i.e. phytoplankton abundance) and water clarity measured as the diffuse attenuation coefficient (1/m) at an *in vacuo* wavelength of 490 nmi (a low diffuse attenuation coefficient indicates high water clarity). Note that, in contrast to sea surface temperature data (Fig. 8), the turbid, plankton-rich water leaving Chesapeake Bay (the "Chesapeake Bay plume") is clearly visible. The Chesapeake Bay plume flows to the south and remains trapped inshore because of the Coriolis effect (Reiss and McConaugha 1999), which is to the right in the Northern Hemisphere. Also visible is the clear oligotrophic mid-Atlantic slope water eastward of the continental shelf.[2] With the exception of fish 4, which made a brief excursion into the mid-Atlantic slope water east of the continental shelf, fish remained in the mid-Atlantic shelf water (i.e. between the extremes of water clarity and phytoplankton abundance immediately to the east and west) (Fig. 9).

Figure 10 presents the frequency histograms for the specific chlorophyll-*a* concentrations and diffuse attenuation coefficients of water occupied by juvenile bluefin tuna. These data confirm that juvenile bluefin tuna restricted their movements primarily to waters with a relatively narrow range of clarity and phytoplankton abundance.

Discussion

Although juvenile bluefin tuna remained within relatively restricted geographical ranges while being tracked (Table 1, Fig. 1), none of these fish showed the repetitive daily behaviors often demonstrated by yellowfin tuna and

[2] Wright, W. R. 1976. Physical oceanography. *In* A summary of environmental information on the continental slope Canadian/United States border to Cape Hatteras, N.C., p. 4-1–4-109. Prepared by TRICOM, The Research Institute of the Gulf of Maine, South Portland, MA, for the Bureau of Land Management, Marine Minerals Division. [Available from National Technical Information Service, U. S. Department of Commerce, Springfield, VA 22161.]

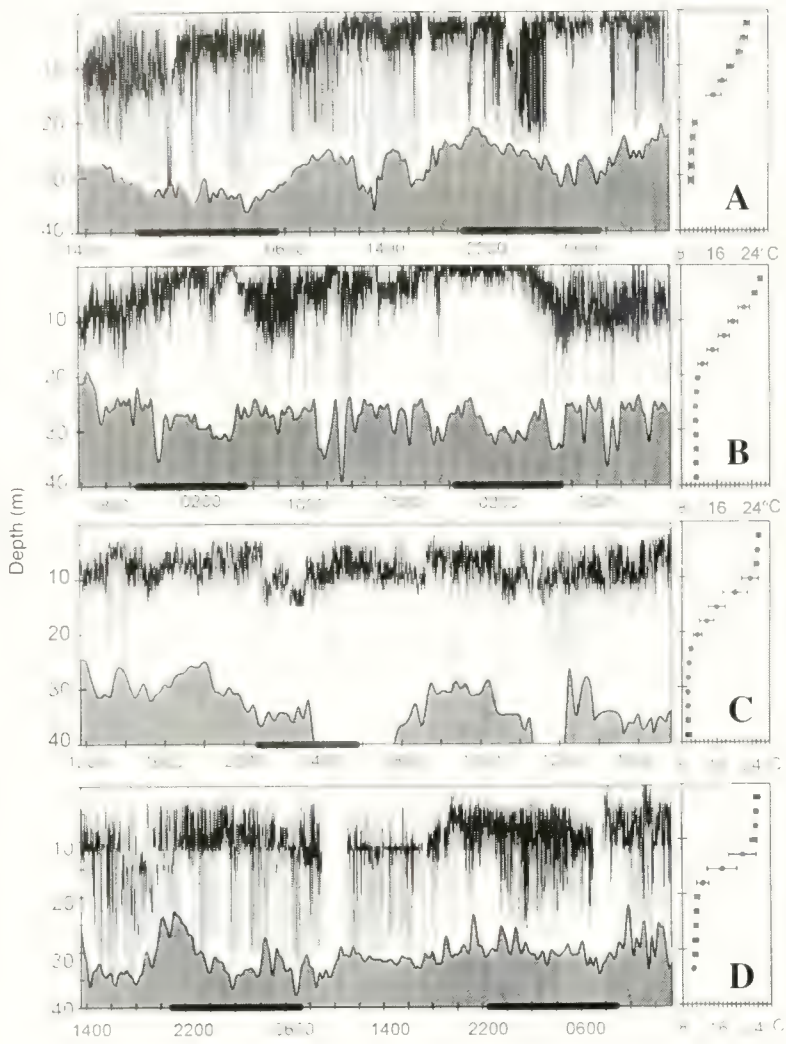

Figure 5

Vertical movements of four juvenile bluefin tuna: (**A**) = fish 1, (**B**) = fish 2, (**C**) = fish 3, (**D**) = fish 5). Bottom topography is shown by the shaded area, and the thick horizontal solid bars indicate nighttime. Depth-temperature profiles (mean ±SEM), recorded during each track by using an expendable bathythermograph (XBT) system, are shown to the right of each vertical movement plot.

skipjack tuna (*Katsuwonus pelamis*). In the Pacific, the latter two species often spend daylight hours associated with reef drop-offs, banks, or man-made fish aggregating devices (FADs), repeatedly move up to ≈5 nmi away at night, then return to the same area the following day (Yuen, 1970; Holland et al., 1990; Marsac and Cayré, 1998; Dagorn et al., 2000a). The continental shelf where the juvenile bluefin tuna were followed is, however, relatively flat compared with the steep topography around the oceanic islands, where many of the yellowfin and skipjack tuna were followed. Unlike the situation in the Pacific, the small topographic features on the mid-Atlantic continental shelf probably do not possess sufficient magnetic signatures that could be detected by the fish (Walker, 1984; Klimley, 1993). Moreover, the movements of the juvenile that we observed closely resembled those of bluefin tuna tracked in the eastern Pacific when they were not near the coast or any apparent significant geological features (Marcinek et al., 2001)

Juvenile bluefin tuna clearly use the entire water column and frequently interact with the bottom when over the continental shelf. Similar behaviors were observed in adult bluefin tuna in the Gulf of Maine (western North Atlantic) (Lutcavage et al., 2000). Frequent vertical movements of juvenile bluefin tuna likely reflect feeding behaviors for capturing sand lance (*Ammodytes* spp.), which

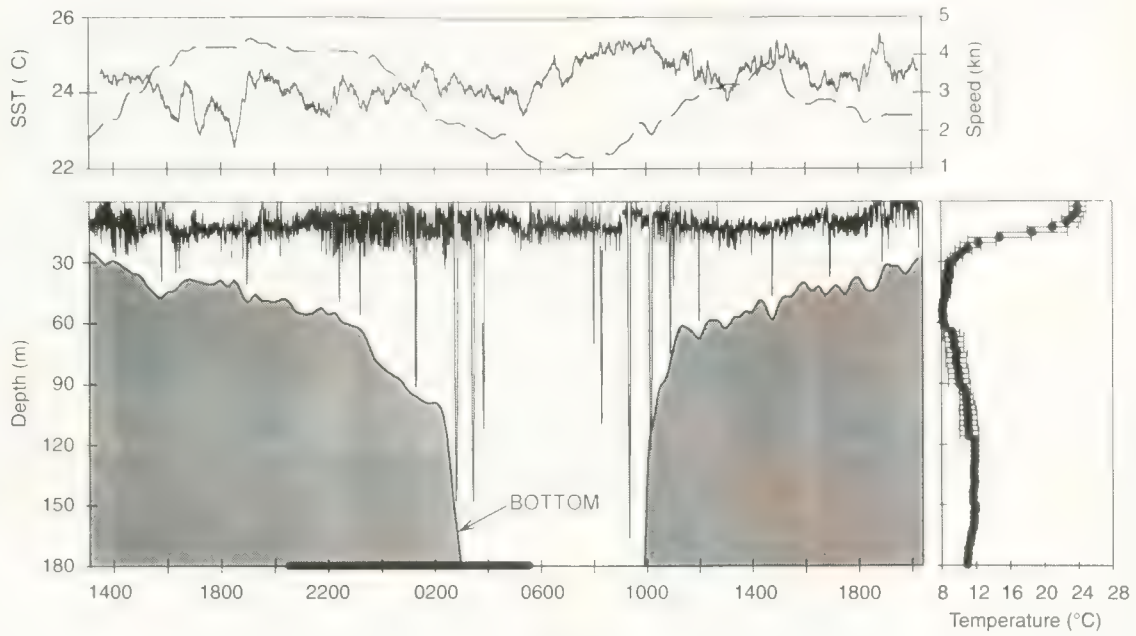

Figure 6

Swimming speed (solid line, upper panel) and vertical movements (lower panel) of fish 4. The change in temperature in the horizontal direction (expressed as sea surface temperature, SST) is shown by the broken line in the upper panel (Brill and Lutcavage, 2001). As in Figure 5, the change in temperature in the vertical direction (mean ±SEM) is shown to the right of the vertical movement plot. Note that changes in swimming speed are not correlated with changes in SST, and that the steepest temperature change the fish could experience moving horizontally (generally less then 0.5°C/km) is several orders of magnitude less then that experienced moving vertically (≈0.6°C/m).

occur throughout the water column during daylight, are abundant in the areas where we tracked the fish, and dominate the diet of tunas in this area (Mason, 1976; Eggleston and Bochenek, 1989). The nature of fish 4's descents up to ≈160 m while off the continental shelf (Fig. 6) remain unclear, although they too may be related to foraging (Dagorn et al., 2000a, 2000b). Their brevity is most likely due to the inability of Atlantic bluefin tuna to withstand temperatures below 10°C for long periods of time, rather than to an intolerance of low ambient oxygen conditions. Although no depth-oxygen profiles were obtained during our study, available data[2] suggest that juvenile tuna did not encounter ambient oxygen levels that were likely to be stressful (Bushnell and Brill, 1991, 1992).

The behavior pattern we observed of short oscillatory dives near the surface is similar to that of both juvenile bluefin tuna in the eastern Pacific (Marcinek et al., 2001) and adult bluefin tuna tracked in the Gulf of Maine (Lutcavage et al., 2000). In all cases, fish spent the majority of their time in the surface layer, although in the Gulf of Maine and eastern Pacific, the temperature of the warmest water available was lower (≈13–22°C) and more variable. As shown in Figure 11, when expressed as the relative change in temperature with depth (i.e. in relation to the surface water temperature occurring during each track), time-at-temperature distributions of juvenile and adult Atlantic bluefin tuna become essentially identical. Moreover, the limiting effects of temperature change on vertical movements are independent of body size. Similarly, yellowfin tuna tracked near the main Hawaiian Islands and off the coast of California occupy the warmest water available, regardless of body size, even though surface water temperature in the two areas differs by more than 5°C (Holland et al., 1990; Block et al., 1997; Brill et al., 1999). Atlantic bluefin tuna, however, are more eurythermal than yellowfin tuna. The latter will rarely expose themselves to more than an 8°C change in temperature, whereas the former regularly subject themselves to a temperature change of up to 13°C (Fig. 11). Surprisingly, the behavior of juvenile bluefin tuna observed by Marcinek et al., (2001) was more like that of yellowfin tuna in that these juvniles would not expose themselves to more then an 8°C temperature change.

It still remains to be conclusively demonstrated, however, whether the vertical movement patterns of tunas and other large pelagic fishes are (as suggested by Brill et al., 1993, 1999) limited by the effects of ambient temperature on cardiac function. Or whether, as suggested by Marcinek et al. (2001), that depth distributions "... may have more to do with the location of prey, and the physiological limitations of the prey, than physiological limitations of the bluefin [tuna]." Moreover, months-long observations

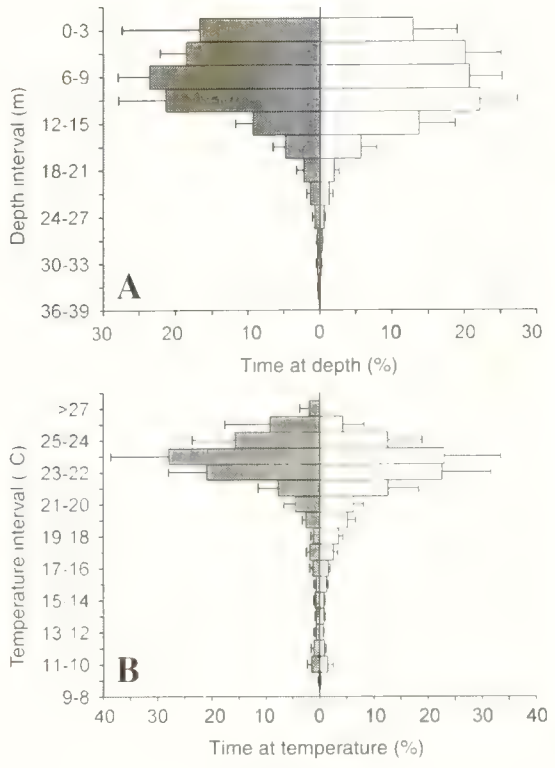

Figure 7

Vertical distribution of five juvenile bluefin tuna expressed as percent time (mean ±SEM) spent at specific depths (**A**) and at specific temperatures (**B**). Shaded bars indicate nighttime and open bars indicate daytime.

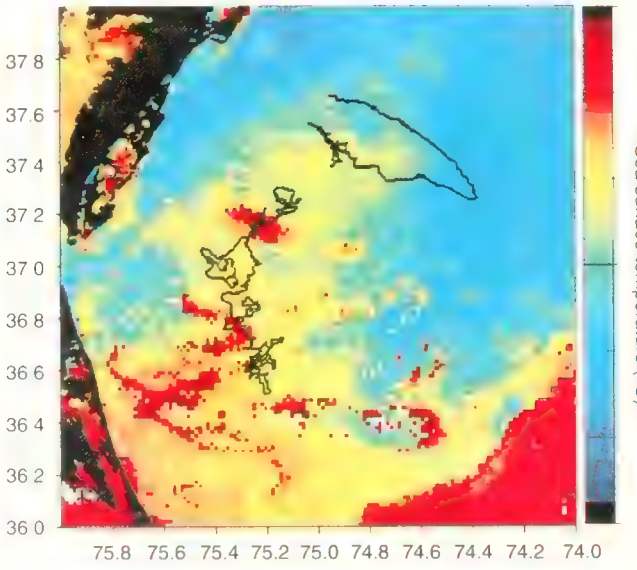

Figure 8

Composite satellite sea surface temperature image (17 June–10 July 1998) and movements of the five juvenile bluefin tuna (Brill and Lutcavage, 2001). Figure reprinted with permission of American Fisheries Society.

of juvenile bluefin tuna in the western Pacific recently obtained with archival (i.e. electronic data recording) tags have shown that the vertical movements of juvenile bluefin tuna can have strong seasonal and geographic components (Kitagawa et al., 2000). In areas and at times (e.g. winter) when there was a strong thermocline, bluefin tuna remained in the uniform-temperature surface layer and demonstrated vertical movement behaviors similar to those observed during the short-term ultrasonic telemetry studies. In the summer, when the themocline was less pronounced, the fish showed very distinct diel periodicity in their vertical movement patterns. They would remain at the surface at night and make rapid vertical movements (from surface to ≈120 m and from ≈21°C to 14°C) during the day. Kitagawa et al. (2000) concluded that the differences in behavior patterns were related to foraging. It is also still an open question as to what extent bluefin tuna's ability to conserve metabolic heat and maintain elevated muscle temperatures (Carey and Teal, 1966) enhances vertical mobility.

Roffer (1987) was apparently the first to propose that movements and abundance of juvenile Atlantic bluefin tuna are controlled by the depth and thickness of the 18.5–20.5°C "preferred habitat" temperature layer. Likewise, Inagake et al. (2001), using archival tags implanted into juvenile bluefin tuna in the western Pacific, found evidence that this temperature range is indeed always "preferred." During the periods of our observations, juvenile bluefin tuna spent the majority of their time (≈80%) in water greater then 22°C. A plausible explanation is that under the conditions of our observation period, juvenile bluefin tuna simply occupy the warmest water available, although a relatively uniform temperature surface layer was evident only during tracks of fish 3, 4, and 5. We also did not find any conclusive indication that juvenile bluefin tuna avoided surface water temperatures above 26°C. Although fish spent less than 20% of time at these temperatures (Fig. 7), less than 20% of the recorded sea surface temperatures (i.e. the warmest water available) were above 26°C.

We also found no relationship between sea surface temperature and horizontal movements (Figs. 6 and 8), although this relationship has been demonstrated for other tuna species in other areas (e.g. Laurs et al., 1977; Fiedler and Bernard, 1987; Uda, 1973). We argue that our results are due to the differences in the vertical and horizontal temperature gradients occurring along the Virginia coast. Juvenile bluefin tuna routinely traveled through the thermocline, moving from the relatively warm surface layer into the mid-Atlantic cold-pool water (Houghton et al., 1982; Houghton and Marra, 1983) underlying it. The fish thus experienced temperature gradients of up to ≈0.6°C/m (Figs. 5 and 6). In contrast, the steepest horizontal temperature gradient in the area where the fish were tracked was approximately three orders of magnitude smaller (≈0.5°C/km). In other words, the frequent vertical movements of juvenile bluefin tuna probably prevent them from detecting and responding to SST gradients.

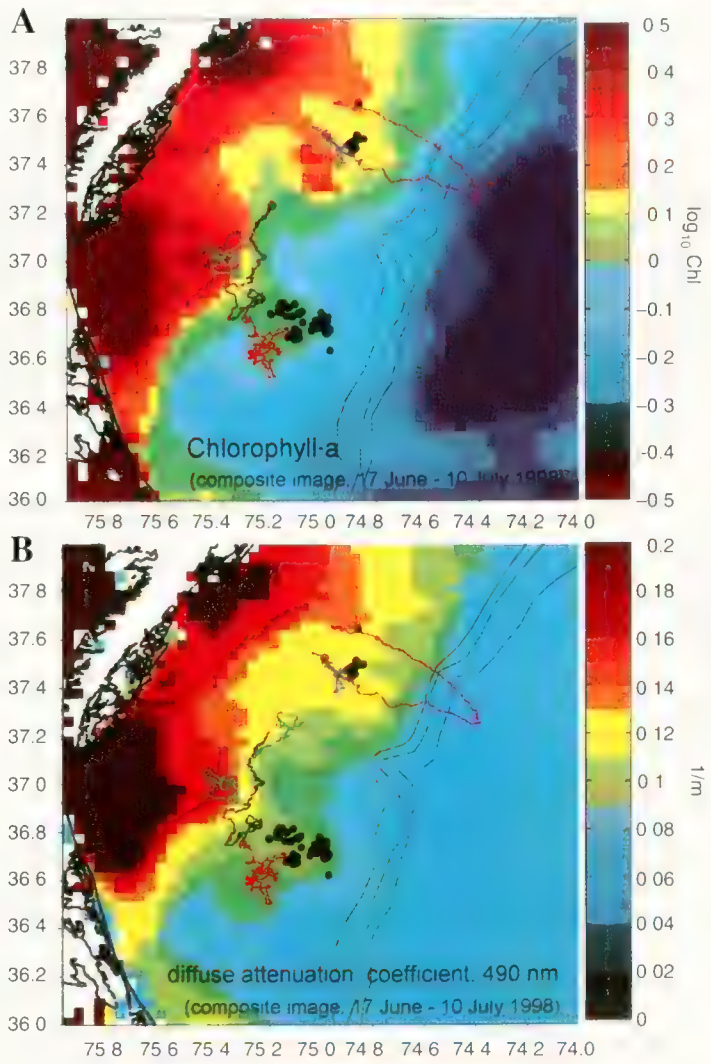

Figure 9

Composite satellite images (17 June–10 July 1998) showing (**A**) chlorophyll-*a* concentrations (mg/m^3) and (**B**) water clarity measured as the diffuse attenuation coefficient (1/m, at an *in vacuo* wavelength of 490 nmi) and movements of the five juvenile bluefin tuna. Locations of juvenile bluefin tuna schools recorded during aerial surveys conducted in 1997 are shown by filled circles. (Lutcavage, M. 1998. Aerial survey of school bluefin tuna off the Virginia Coast, July 1997. Report to the National Marine Fisheries Service, cooperative agreement NA77fm0533. [Available from the author, Edgerton research Laboratory, New England Aquarium, Central Wharf, Boston, MA 02110].) are shown by filled circles. The edge of the continental shelf is indicated by the 50-, 100-, and 200-m isobath lines (Brill and Lutcavage, 2001). Figure reprinted with permission of American Fisheries Society.

Carey (1992) was one of the first to appreciate the importance of vertical thermal structuring and stated "Temperature gradients of 15° to 20°C are not uncommon within the depth ranges of pelagic fish. By moving a few hundred meters vertically, an animal may encounter a greater temperature change than it experiences seasonally or in moving thousands of miles horizontally." As with bluefin tuna, the vertical movements of yellowfin tuna and swordfish also result in their experiencing vertical temperature gradients orders of magnitude greater than horizontal temperature gradients (Carey and Robison, 1981; Carey, 1990; Holland et al., 1990; Cayré and Marsac, 1993). The inabil-

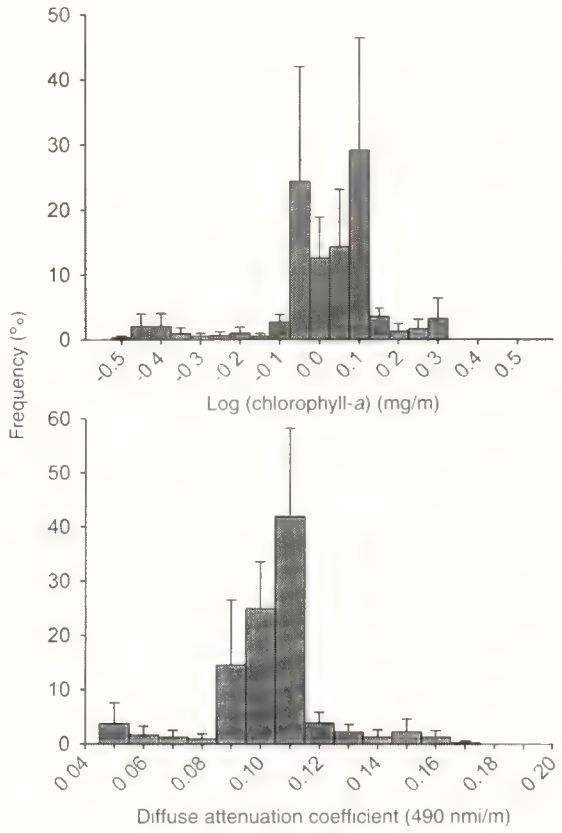

Figure 10

Frequency histogram (mean ±SEM) of chlorophyll-*a* concentrations (mg/m^3) and water clarity measured as the diffuse attenuation coefficient (1/m, at an *in vacuo* wavelength of 490 nmi) in waters along the track lines of five juvenile bluefin tuna (Brill and Lutcavage, 2001). The span of the horizontal axes show the approximate range of these variables present off the eastern shore of Virginia.

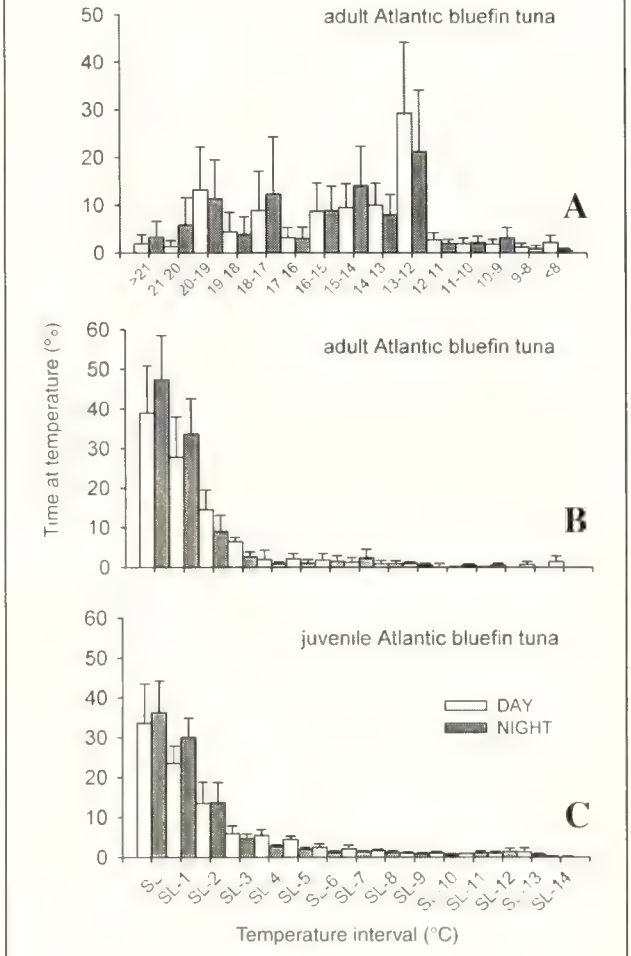

Figure 11

Frequency histograms (mean ±SEM) showing time spent at specific temperatures by adult bluefin tuna tracked in the Gulf of Maine (western North Atlantic) with temperatures expressed as water temperature (**A**), and with temperatures expressed in relation to surface layer temperature (**B**), data taken from Lutcavage et al., 2000). Equivalent data for juvenile bluefin tuna are presented in panel **C**. Shaded bars indicate nighttime and open bars indicate daytime.

ity of fish to sense shallow horizontal temperature gradients in the face of the steep vertical temperature gradients they routinely experience may explain, therefore, why Power and May (1991) and Podestá et al. (1993) could find no correlation between SST "fronts" and the apparent abundance of yellowfin tuna in the Gulf of Mexico and swordfish in the western north Atlantic.

In contrast to SST, water clarity and phytoplankton abundance appear to have a strong influence on the horizontal movements of juvenile bluefin tuna (Figs. 9 and 10). Tunas are sight hunters, and possess the highest visual acuity of any teleost (Nakamura, 1968). We suspect that juvenile bluefin tuna remain in water masses with a standing phytoplankton biomass sufficient to support concentrations of prey, but where turbidity is low enough that visual prey detection and prey capture abilities are not impeded. Our conclusion is further supported by the locations of juvenile bluefin tuna schools detected in aerial surveys conducted in 1997.[3] Although satellite data showing diffuse attenuation coefficients and chlorophyll-*a* concentrations are not available for 1997, bluefin tuna schools were located in the areas where the fish carrying ultrasonic transmitters remained (Fig. 9). Olson and Podestá (1987), Olson et al. (1994), and Humston et al. (2000) have also concluded that aggregations of highly mobile species

[3] Lutcavage, M. 1998. Aerial survey of school bluefin tuna off the Virginia Coast, July 1997. Report to the National Marine Fisheries Service (cooperative agreement NA77FM0533). [Available from the author, Edgerton Research Laboratory, New England Aquarium, Central Wharf, Boston, MA 02110.]

at fronts result from cues other than SST, such as changes in the photic environment associated with phytoplankton distribution, changes in prey abundance, or enhanced forage opportunities.

Aerial survey techniques and population assessments of juvenile bluefin tuna

Techniques for interpretation of aerial survey data with respect to population assessments are complex (e.g. Lo et al., 1999; Newlands and Lutcavage, 2001), and a thorough discussion is beyond the scope of our present study. We can, however, use our data on juvenile bluefin tuna's vertical movements and distribution patterns to provide some inferences as to how often they are likely to be visible at the ocean's surface or detectable at a specific depth. Juvenile bluefin tunas spent less than 13% of daylight hours at depths of 0–3 m (Fig. 7), where visual or photographic detection is possible. The depth distribution of juvenile fish was similar to that of adult bluefin tuna tracked in the Gulf of Maine (12% of daylight hours at depths of 0–4 m; Lutcavage et al., 2000). Abundance estimates based solely on photographic data will, therefore, have to be corrected to account for the significant number of fish that maybe be present, but that are beyond detection range. Fish detection systems that use lasers (the so called "light detection and range" or "LIDAR" systems) are expected to have a depth detection zone of up to 60 m (Oliver et al., 1994). This detection zone encompasses almost the entire water column over the sections of continental shelf where juvenile bluefin tuna are likely to be found. Moreover, if the behavior of the fish that moved into deeper water off the continental shelf is assumed typical, then juvenile bluefin tuna would be detected by LIDAR systems even in deep water. The relatively small net displacement distance (i.e. distance between start and end points, Table 1) may require the development of filtering algorithms to reduce errors caused by double counting if parallel transects are flown less than ≈50 km apart, or if the same area is resurveyed weekly or more often. Conversely, significant fish aggregations could be missed if parallel transects are too widely spaced.

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Differences in diet of Atlantic bluefin tuna (*Thunnus thynnus*) at five seasonal feeding grounds on the New England continental shelf*

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Abstract—The stomachs of 819 Atlantic bluefin tuna (*Thunnus thynnus*) sampled from 1988 to 1992 were analyzed to compare dietary differences among five feeding grounds on the New England continental shelf (Jeffreys Ledge, Stellwagen Bank, Cape Cod Bay, Great South Channel, and South of Martha's Vineyard) where a majority of the U.S. Atlantic commercial catch occurs. Spatial variation in prey was expected to be a primary influence on bluefin tuna distribution during seasonal feeding migrations. Sand lance (*Ammodytes spp.*), Atlantic herring (*Clupea harengus*), Atlantic mackerel (*Scomber scombrus*), squid (Cephalopoda), and bluefish (*Pomatomus saltatrix*) were the top prey in terms of frequency of occurrence and percent prey weight for all areas combined. Prey composition was uncorrelated between study areas, with the exception of a significant association between Stellwagen Bank and Great South Channel, where sand lance and Atlantic herring occurred most frequently. Mean stomach-contents biomass varied significantly for all study areas, except for Great South Channel and Cape Cod Bay. Jeffreys Ledge had the highest mean stomach-contents biomass (2.0 kg) among the four Gulf of Maine areas and Cape Cod Bay had the lowest (0.4 kg). Diet at four of the five areas was dominated by one or two small pelagic prey and several other pelagic prey made minor contributions. In contrast, half of the prey species found in the Cape Cod Bay diet were demersal species, including the frequent occurrence of the sessile fig sponge (*Suberites ficus*). Prey size selection was consistent over a wide range of bluefin length. Age 2–4 sand lance and Atlantic herring and age 0–1 squid and Atlantic mackerel were common prey for all sizes of bluefin tuna. This is the first study to compare diet composition of western Atlantic bluefin tuna among discrete feeding grounds during their seasonal migration to the New England continental shelf and to evaluate predator-prey size relationships. Previous studies have not found a common occurrence of demersal species or a predominance of Atlantic herring in the diet of bluefin tuna.

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Atlantic bluefin tuna (*Thunnus thynnus*) are widely distributed throughout the Atlantic Ocean and have attracted valuable commercial and recreational fisheries in the western North Atlantic during the latter half of the twentieth century. The western North Atlantic population is considered overfished by the International Commission for the Conservation of Atlantic Tunas (NMFS, 1999). Bluefin tuna are the largest scombrid species, and the largest teleost occurring in the Gulf of Maine (Bigelow and Schroeder, 1953). Bluefin tuna migrate to coastal waters off New England during warmer months, feeding on local concentrations of prey. This migration supports a major component of the U.S. Atlantic commercial fishery for bluefin tuna; from 1978 to 1992 New England accounted for between 73% and 98% of annual commercial landings (Chase, 1992; and NMFS, 1995). Substantial annual variation has been seen in the harvest locations on the New England continental shelf (Chase, 1992). Spatial variation in prey populations is suspected to be the primary influence on these annual aggregations of bluefin tuna. Adaptations in the circulatory system of the bluefin tuna allow these fish to retain metabolic heat, facilitating the regulation of body temperature (Carey and Teal, 1969) and assisting in the efficient transfer of energy from consumed prey to fast growth rates and large body size. These adaptive features also allow bluefin tuna to make extensive migrations into cold-temperate waters in search of prey. Diet information is necessary to improve the understanding of seasonal movements of bluefin tuna and predator-prey relationships in the New England continental shelf region, and as a baseline for bioenergetic analyses. Information on the feeding habits of this economically valuable species and apex predator in the western North Atlantic Ocean is limited, and nearly absent for the seasonal feeding grounds where most U.S. Atlantic commercial catches occur.

Previous food habit studies have shown that western North Atlantic bluefin tuna are opportunistic feeders on a wide variety of finfish, cephalopods, and crustaceans (Crane, 1936; Krumholz, 1959; Dragovich, 1970; Mason, 1976; Holliday, 1978; Eggleston and Bochenek, 1990; Matthews et al.[1]). Pinkas (1971) reported similar results for Pacific bluefin tuna (*Thunnus thynnus orientalis*). These bluefin tuna food habit studies either reported on small numbers of samples or were qualitative studies on samples distributed over a broad geographic range. Previous studies have not evaluated size relationships between bluefin tuna and their prey and the amount of food consumed. The present study targeted regions of the New England giant tuna (>140 kg) fishery to quantitatively analyze stomach contents of bluefin tuna among discrete seasonal feeding grounds and to investigate predator-prey size relationships for this species in the Gulf of Maine.

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[1] Matthews, F. D., D. M. Damkaer, L. W. Knapp, and B. B. Collette. 1977. Food of western North Atlantic tunas (*Thunnus*) and lancetfish (*Alepisaurus*). Nat. Oceanic Atmos. Admin. Tech. Rep. NMFS SSRF-706, Washington, D.C., 19 p.

Materials and methods

Study area

Five fishery areas (Jeffreys Ledge, Stellwagen Bank, Cape Cod Bay, Great South Channel, and South of Martha's Vineyard [Fig. 1]) were selected for their traditional association with the bluefin fishery and because geographic and bathymetric differences among areas could result in distinct prey communities. The northernmost area, Jeffreys Ledge, is a major bathymetric feature in the Gulf of Maine and is important for commercial fisheries from northern Massachusetts, New Hampshire, and southern Maine. Stellwagen Bank is a distinct bathymetric ridge located on the eastern boundary of Massachusetts Bay (DOC[2]) that provides close access for ports from Gloucester to Cape Cod. Cape Cod Bay is a large, relatively shallow Gulf of Maine bay that is semi-enclosed on three sides by the land mass of Cape Cod and the south shore of Massachusetts. The two southern areas, Great South Channel and the area south of Martha's Vineyard, are larger regions with less distinct bathymetric features and are separated by Nantucket Shoals. The Great South Channel covers a wide nearshore region running east of Chatham and Nantucket and is bordered by the slopes of Nantucket Shoals on the west. The area south of Martha's Vineyard is located on the continental shelf off southern New England and is distinguished from the other areas by its warmer water, predominance of smaller bluefin tuna (<50 kg), and the seasonal occurrence of other large pelagic fish, such as marlins and tropical tunas.

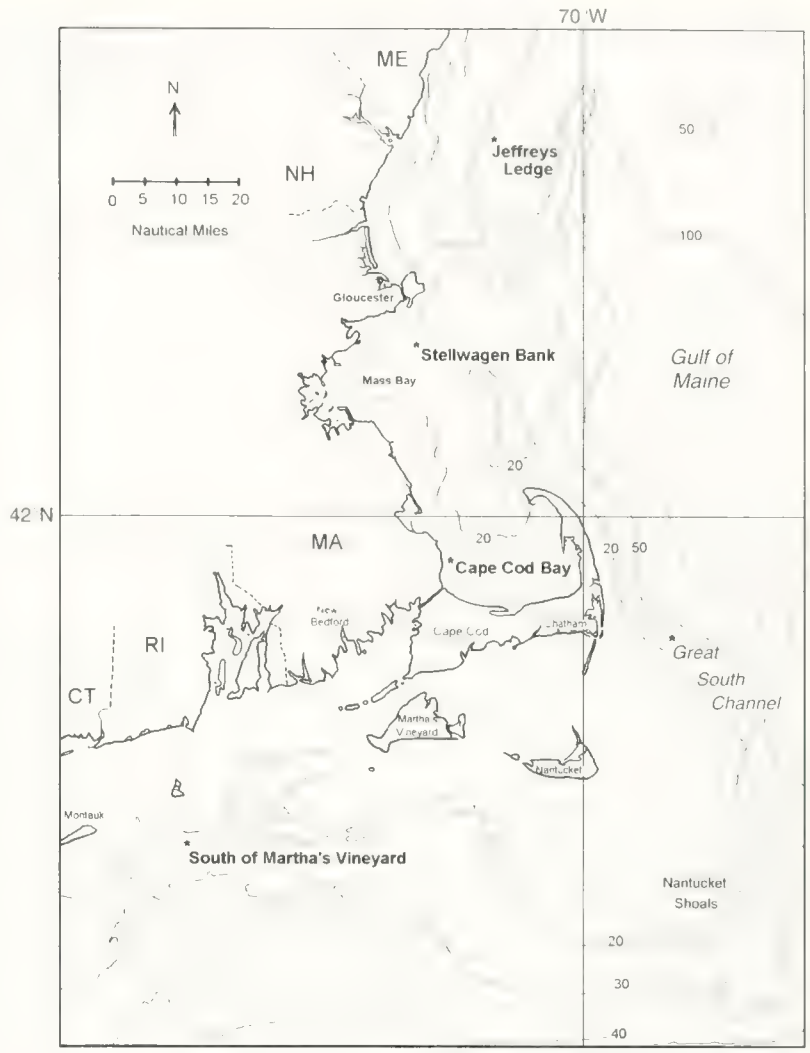

Figure 1

Map of the five bluefin tuna feeding grounds used as study areas (★) July–October 1988–92. Depths are given in fathoms.

Commercial catch records and trawl survey indices of abundance indicate that Atlantic herring (*Clupea harengus*) and Atlantic mackerel (*Scomber scombrus*) are the principal pelagic fish species for all these study areas (Clark and Brown, 1976; and NOAA, 1998). Atlantic herring occur in lower relative abundance in the region south of New England than in northern regions. Jeffreys Ledge and Great South Channel are primary spawning locations for Atlantic herring. Catch records and trawl survey indices indicate that the following prey species have been abundant in the study areas: silver hake (*Merluccius bilinearis*), butterfish (*Peprilus triacanthus*), northern shortfin squid (*Illex illecebrosus*), and longfin inshore squid (*Loligo pealeii*).

Sample collection and analysis

Bluefin stomach samples were collected primarily from commercial landings at ports in Massachusetts during the 1988–92 seasons (July–October). Sportfishing tournaments were a secondary source of stomach samples. Handgear landings (rod and reel, handline, and harpoon) were primarily collected in Gloucester and Cape Cod. Purse-seine landings were also a large source of samples, and were collected in Gloucester, New Bedford, and Cape Cod. A majority of stomach samples was collected during 1989 and 1990. A reduced number of samples after 1990 was influenced by the increasing practice of gutting bluefin at sea to sustain a quality product for the sashimi export market.

Most samples were collected at the docks and processing locations of commercial tuna buyers. The vessel captain or tuna buyer was interviewed for location of catch.

[2] DOC (Department of Commerce). 1991. Stellwagen Bank National Marine Sanctuary, Draft environmental impact statement/management plan. U.S. Dep. Commerce (DOC), Nat. Oceanic Atmos. Adm., Sanctuaries and Reserves Division, Washington, D.C., 238 p.

The curved fork length (CFL) and weight of the catch were recorded from the National Marine Fisheries Service (NMFS) tuna logbook. Stomachs were removed by cutting the esophagus above the pylorus and were stored on ice until analysis later that day or were frozen for analysis at a later date. Stomach samples were typically removed from bluefin tuna the day of capture, except those from purse-seine landings, where the catch was often submerged in ice for one or two days prior to landing.

Stomach contents were identified to the lowest possible taxon and weights and counts were made of individual prey species. Wet weights of prey were measured with Homs tubular scales (±5 g) after contents were rinsed through a standard testing sieve (2.00-mm mesh). Prey counts were made only when all individual prey items could be identified and counted for a given stomach sample. Because bluefin tuna consume relatively large prey items and swallow prey whole, species identification was possible for nearly all contents. Skeletal remains were compared with the skeletons of known specimens to assist with identification. Fish contents that could not be identified were categorized as "unidentified fish." Otoliths, squid beaks, and skeletal traces less than 5 g were rounded up to a minimum weight of 5 g.

Stomach-contents data were analyzed by frequency of occurrence, percent composition by number, and percent composition by weight for each prey item (Hyslop 1980; Bowen 1986). Frequency of occurrence can indicate prey composition and availability, and number and weight percentages can represent the quantity a prey item contributes to a diet. "Stomach-contents biomass" refers to all prey in stomach contents, and "prey weight" refers to the weight of individual prey species.

Stomach samples were assigned a status of "empty," "chum," "chum and prey," or "prey only." Chum refers to cut pieces of bait fish that fishermen use to attract bluefin. Both empty and chum stomach samples were eliminated from further data analysis. For "chum and prey" stomachs, chum weight was eliminated from the analysis, and prey weight was included because chum and natural prey were easily distinguished in bluefin tuna stomachs. When the status of contents, or the veracity of catch location could not be resolved, the samples were eliminated from the analysis.

Statistical analysis

Stomach-contents biomass data were analyzed to determine differences among the five fishery areas. Prey weight data were tested for normality (Shapiro and Wilk, 1965) and equality of variance (BMDP, 1990). Stomach-contents biomass data were transformed to natural logarithms and tested for area differences by using the Brown-Forsythe test for unequal variances and the Welch test for pairwise comparisons of areas (BMDP, 1990).

The species composition of stomach contents were tested among areas with the Spearman rank correlation test, under the null hypothesis of no association between species composition and feeding area. The twelve most common prey species were ranked according to frequency of occurrence for each location. The Spearman rank correlation test was applied by pairwise ranking for all locations, excluding missing cases.

Bluefin tuna size was compared with prey length and stomach-contents biomass data by using the Pearson product moment correlation coefficient (Sokal and Rohlf, 1981) to test for significant associations between prey and predator length, and to correlate bluefin tuna weight and stomach-contents biomass for all samples from the Gulf of Maine. The relationship between bluefin tuna size and food consumed was also evaluated by comparing the ratio of stomach-contents biomass and tuna weight (% kg wet weight of prey biomass/kg wet weight of tuna) to tuna length (curved fork length) (Young et al., 1997). The area south of Martha's Vineyard area was excluded from tests on size relationships because of the limited sample numbers of juvenile bluefin tuna collected there.

Results

A total of 819 bluefin tuna stomachs were analyzed during 1988–92 (Table 1) and 568 contained prey; empty stomachs (206) and "chum only" samples (45) were eliminated from further analysis. Approximately equal quantities of the samples with prey came from purse-seine landings (273) and from rod and reel and handline landings (264). The fishing method used for the hook-and-line landings was recorded for 242 samples and was evenly divided between chumming (where chum was used as bait) (123) and trolling (119). Size composition of sampled bluefin tuna was similar for the four Gulf of Maine study areas; a large majority of fish were large, mature adults, estimated to be age 10 and older (Mather and Schuck, 1960). In contrast, nearly all fish sampled from the area south of Martha's Vineyard were small juveniles, ages 2–6. Tuna sampled from Cape Cod Bay had the largest average size (251 cm CFL, and 273 kg).

Prey composition

All areas combined Stomach contents comprised at least 21 species of teleosts, two species of elasmobranchs, and at least nine species of invertebrates (Table 2). Stomach-contents biomass in terms of taxonomic composition was dominated by *Osteichthyes* (Fig. 2A). Of the invertebrates, only squid ("squid" refers to two species, *Loligo pealei* and *Illex illecebrosus*) were a consistent component of prey composition. Although squid accounted for only about 2% of the stomach-contents biomass, it was the second most common prey, occurring in a third of all stomach samples. The only other common invertebrate was the fig sponge (*Suberites ficus*) found in Cape Cod Bay. Despite the large diversity of prey items, few species made major contributions to overall prey composition. Sand lance (*Ammodytes ssp*), squid, Atlantic herring, Atlantic mackerel, and bluefish (*Pomatomus saltatrix*) exceeded all other prey in terms of frequency of occurrence and accounted as a group for 88% of total stomach-contents biomass (Fig. 2B). In the Gulf of Maine areas, sand lance, and Atlantic herring were the major prey in the diet of bluefin tuna during

Table 1

Summary of number of bluefin tuna stomach samples collected at five study areas on the New England continental shelf, July–October 1988–92. Also included are lengths (curved fork length [CFL], cm) and weights (kg) of sampled tuna. "Other" column refers to twelve samples with prey collected at nearshore fishing areas in the Gulf of Maine that were outside the five study areas

Sample category	Jeffreys Ledge	Stellwagen Bank	Cape Cod Bay	Great South Channel	South of Marths's Vineyard	Other	Total
By year							
1988	13	30	16	0	0	0	59
1989	13	33	28	88	13	1	176
1990	57	15	26	61	33	2	194
1991	34	8	13	34	2	8	99
1992	6	7	26	0	0	1	40
By condition of stomach							
Number with prey	123	93	109	183	48	12	568
Number with chum	19	17	6	0	1	2	45
Number empty	5	1	158	27	8	7	206
Total	147	111	273	210	57	21	819
Mean length of tuna	221	240	251	221	124	221	227
SD	32	35	19	38	30	37	44
Mean weight of tuna	186	243	273	196	36	205	215
SD	78	94	58	90	38	83	97

the study period. Twenty-one bluefin tuna stomach samples were collected outside of the five study areas; mostly at two inshore locations north of Gloucester and south of Stellwagen Bank.

Jeffreys Ledge Atlantic herring were the dominant prey in the 123 stomach samples from Jeffreys Ledge (Table 3). The frequency of occurrence for Atlantic herring (74%) was the second highest and the percentage of stomach-contents biomass (87%) was the highest for any individual prey item among areas. Squid were in nearly half of all samples, but comprised less than 2% of stomach-contents biomass. Atlantic mackerel were the third most common prey for this region (32% occurrence). All other prey species occurred incidentally. Menhaden (*Brevoortia tyrannus*) and pollock (*Pollachius virens*) were unique to samples from Jeffreys Ledge. Mean stomach-contents biomass (~2.0 kg) was the highest among study areas and few empty stomachs were found.

Stellwagen Bank As at Jeffreys Ledge, a single species dominated the stomach-contentss from Stellwagen Bank. Sand lance were found in nearly 80% of 93 stomachs and accounted for nearly 70% of the stomach-contents biomass (Table 3). Atlantic herring, squid, spiny dogfish (*Squalus acanthias*), Atlantic mackerel, and bluefish tuna were secondary prey items, with frequencies of occurrence ranging from 9% to 14%. All other prey species found in stomach contents from Stellwagen Bank occurred incidentally, and there were no species from this area that were unique to the overall study area.

Cape Cod Bay Unlike diet composition for the other study areas, diet composition for Cape Cod Bay did not indicate a dominant pelagic prey but did include the common occurrence of demersal prey. Six prey species were only found in Cape Cod Bay. Squid occurred most frequently but accounted for only 2% of stomach-contents biomass biomass (Table 3). The fig sponge was the top prey in terms of percentage by weight (27%). The diet of bluefin tuna caught in Cape Cod Bay displayed the most diversity among study areas. A total of 16 prey species were identified, of which eight were demersal species. Three species of flounder were identified, representing 9% of the stomach-contents biomass. The occurrence of bluefish tuna as prey in Cape Cod Bay (25%) was the highest among study areas. The amount of food in Cape Cod Bay stomach samples was the lowest for the four Gulf of Maine locations; 60% of the stomachs collected from this area were empty.

Great South Channel A large number of stomach samples with prey (183) were collected from the Great South Channel during 1989–91. The most abundant prey was sand lance, occurring in 62% of the stomach samples and accounting for 28% of the stomach-contents biomass. Atlantic herring was also important, with a frequency of occurrence of 27% and stomach-contents biomass of 48%. As with Stellwagen Bank and Jeffreys Ledge, squid was an important secondary prey item, and bluefish and Atlantic mackerel were secondary prey of lesser importance. Four species were unique to Great South Channel samples: shrimp (*Pandalus* spp.), finger sponge (*Haliclona oculata*), silverstripe halfbeak (*Hyporhamphus unifasciatus*), and Atlantic cod (*Gadus morhua*).

South of Martha's Vineyard Only 48 stomachs with prey were analyzed from the area south of Martha's Vineyard.

Table 2

Stomach contents of bluefin tuna caught off New England during 1988–92. Prey species are combined for all five study areas, including 12 samples from outside of the study areas. Percent frequency of occurrence (% O) and percent weight (% W) data were determined from the 568 stomach samples that contained prey.

Prey species		Frequency of occurrence	Total weight (g)	% O	% W
Sand lance	*Ammodytes* (spp.)	194	128,240	34.2	22.6
Atlantic herring	*Clupea harengus*	167	299,550	29.4	52.8
Atlantic mackerel	*Scomber scombrus*	108	18,930	19.0	3.3
Bluefish	*Pomatomus saltatrix*	55	40,830	9.7	7.2
Butterfish	*Peprilus triacanthus*	21	1685	3.7	0.3
Silver hake	*Merluccius bilinearis*	16	1490	2.8	0.3
Windowpane	*Scopthalmus aquosus*	12	1890	2.1	0.3
Hake	*Urophycis* (spp.)	11	2500	1.9	0.4
Winter flounder	*Pseudopleuronectes americanus*	8	1820	1.4	0.3
Atlantic menhaden	*Brevoortia tyrannus*	7	5500	1.2	1.0
Sea horse	*Hippocampus erectus*	7	40	1.2	<0.05
Atlantic cod	*Gadus morhua*	6	22,840	1.1	4.0
Fourspot flounder	*Paralichthys oblongus*	2	370	0.4	0.1
American plaice	*Hippoglossoides platessoides*	2	310	0.4	0.1
Wrymouth	*Cryptacanthodes maculatus*	2	1300	0.4	0.2
Pollock	*Pollachius virens*	1	940	0.2	0.2
Filefish	*Monocanthus hispidus*	1	30	0.2	<0.05
Halfbeak	*Hyporhamphus unifasciatus*	1	120	0.2	<0.05
Longhorn sculpin	*Myoxocephalus octodecimspinosus*	1	280	0.2	<0.05
Unidentified fish	Teleostei	34	605	6.0	0.1
Spiny dogfish	*Squalus acanthias*	13	10,490	2.3	1.9
Skate	*Raja* (spp.)	13	4670	2.3	0.8
Skate egg case	*Raja* (spp.)	3	20	0.5	<0.05
Squid	Cephalopoda	186	10,835	32.8	1.9
Octopus	Cephalopoda	1	30	0.2	<0.05
Shrimp	*Pandalus* (spp.)	5	25	0.9	<0.05
Lobster	*Homarus americanus*	2	230	0.4	<0.05
Argonaut	*Argonauta argo*	2	25	0.4	<0.05
Crab	*Cancer* (spp.)	2	15	0.4	<0.05
Salp	Salpidae	2	60	0.4	<0.05
Fig sponge	*Suberites ficus*	30	11,510	5.3	2.0
Finger sponge	*Haliclona oculata*	1	50	0.2	<0.05
Stomachs with chum and prey		95	107,430 (chum)		
Stomachs with chum only		45	49,040 (chum)		
Empty stomachs		206	—		
Total stomachs with prey		568	567,230		
Total stomachs sampled		819	723,700		

Giant bluefin were scarce in this area during the study period and numerous samples could not be used because the bluefin tuna were caught in association with trawler fleet discards. This area is distinguished from the others by a predominance of juvenile bluefin tuna . Four prey species were unique to this area: lined sea horse (*Hippocampus erectus*), argonaut (*Argonauta argo*), planehead filefish (*Monocanthus hispidus*), and octopus (Cephalopoda). The filefish and seahorse were associated with bluefin tuna foraging at sargassum weed communities. Squid and Atlantic mackerel were the two most important prey for this area. The frequency of occurrence and percentage of prey weight for mackerel and butterfish were the highest among study areas. Combined stomach-contents biomass for squid, mackerel, and butterfish represented nearly 80% of the stomach contents for this area.

Comparison of study areas The top 12 prey items, overall, were ranked for each area by frequency of occurrence, and area differences were tested with Spearman rank correlation. Of the ten pairwise comparisons, only Stellwagen Bank and Great South Channel showed a significant association in the ranking of prey items (r=0.98, P<0.02), attributable to a high rank of sand lance and a similar ranking of squid, Atlantic herring, and Atlantic mackerel for both areas.

Stomach-contents biomass

Comparison of study areas Large differences in stomach-contents biomass were found: Jeffreys Ledge averaged nearly 2 kg, followed by approximately 1 kg for Stellwagen Bank and Great South Channel, and less than 0.5 kg for the remaining areas. Stomach-contents biomass data from the five areas were positively skewed and heteroscedastic. The natural logarithm-transformed data for Stellwagen Bank, Cape Cod Bay, and Great South Channel were normal (Wilk-Shapiro test, P>0.05). Transformed biomass data for the other two areas still differed significantly from normality. Transformation of biomass data reduced the inequality of variances, but significant differences (Levene's test, P<0.05) remained, which precluded use of analysis of variance. The Brown-Forsythe test for unequal variances showed a significant effect of area on stomach-contents biomass (P<0.0001). Pairwise comparisons of the equality of prey weight means were made with the Welch test (Bonferroni corrected significance level of P=0.005). All area pairwise comparisons of stomach-contents biomass were significantly different except that between Cape Cod Bay and Great South Channel (P=0.816).

The similarity in the amount of food found at Cape Cod Bay and Great South Channel was also indicated by the geometric mean of stomach-contents biomass (Table 4). The arithmetic mean of stomach-contents biomass was higher at the Great South Channel than Cape Cod Bay, but this value was biased by a few samples with large amounts of prey. The stomach-contents biomass range for Cape Cod Bay did not exceed 3.0 kg, in contrast to the wider range for the Great South Channel up to 16.0 kg, including 13 samples over 3.0 kg. The use geometric means reduced the bias of skewness and indicated that samples from Jeffreys Ledge contained the most prey and that the amounts declined moving southward.

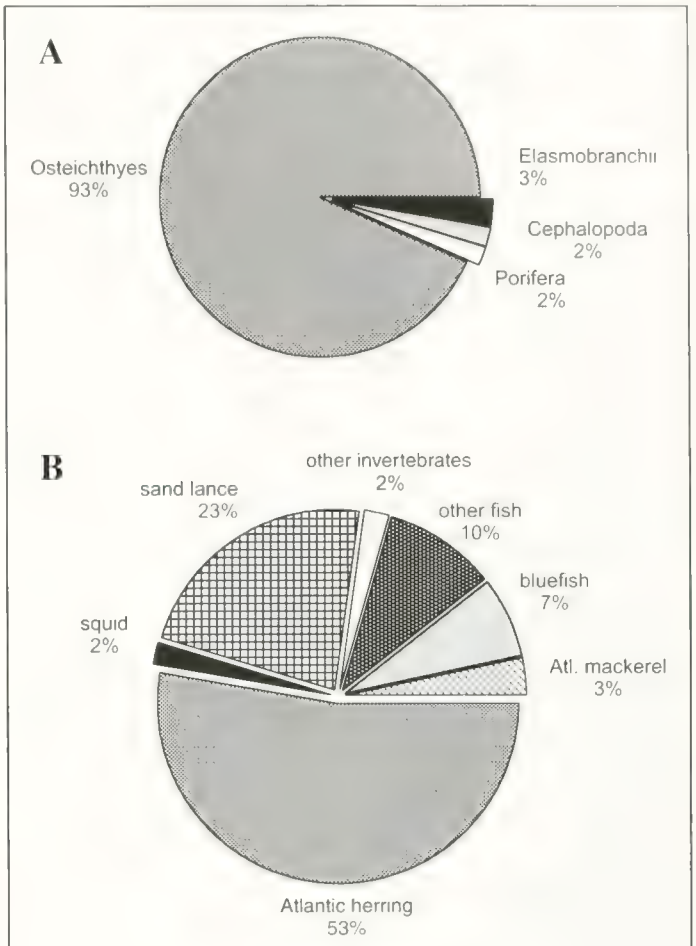

Figure 2

Percent prey weight composition in stomach contents of bluefin tuna caught off New England during 1988–92 (n=568). The taxonomic composition (**A**) includes 0.05% Crustacea and 0.01% Urochordata. The comparison by major prey type (**B**) comprises the five most common prey and all remaining fish and invertebrates.

Effect of tuna size Increased stomach-contents biomass with increasing body size (due to increasing gape and stomach size) was not clearly demonstrated from these data. Correlation of stomach-contents biomass to bluefin weight was not significant for Gulf of Maine samples. A scatterplot of data for the Gulf of Maine samples revealed that a large majority of the samples contained small amounts of food, regardless of body size (Fig. 3). A size-related trend was observed in that only very large bluefin tuna (>250 kg) contained more that 6 kg of food. Size effects were also compared by using the ratio of stomach-contents biomass and tuna weight (% kg/kg, wet weight) to tuna length. The percentage of food to body mass declined with increasing bluefin tuna length (Fig. 4). Food observed in 120–149 cm bluefin tuna averaged over 1% of their body weight, and declined to approximately 0.5% for bluefin tuna over 230 cm. The high ratios primarily resulted from large meals of Atlantic herring or sand lance. Cape Cod Bay ratios were consistently the lowest among the four areas, ranging from 0.1 to 0.2%.

Characteristics of prey species

Prey size Prey size was evaluated for 190 stomach samples that contained measurable prey from the four Gulf of Maine areas. A total of 1866 prey items were measured, of which 95% were either sand lance, Atlantic herring, squid, or Atlantic mackerel (Table 5). A significant positive cor-

Table 3

Stomach contents of bluefin tuna caught off New England during 1988-1992, listed by the five study areas. Percent frequency of occurrence (% O) and percent by weight (% W) were calculated for each prey species.

	Jeffreys Ledge		Stellwagen Bank		Cape Cod Bay		Great South Channel		South of Martha's Vineyard	
Prey species	% O	% W	% O	% W	% O	% W	% O	% W	% O	% W
Sand lance	3.3	1.8	79.6	69.3	0	0	62.3	28.3	0	0
Atlantic herring	74.0	87.2	14.0	6.0	8.3	3.1	27.3	48.4	2.1	2.5
Atlantic mackerel	31.7	2.0	10.8	2.6	18.3	12.7	8.2	0.6	33.3	56.2
Bluefish	7.3	3.5	8.6	17.5	24.8	14.7	4.9	5.7	0	0
Butterfish	2.4	<0.05	1.1	<0.05	5.5	1.5	1.6	0.2	16.7	10.4
Silver hake	3.3	0.2	0	0	0	0	2.2	0.3	10.4	2.9
Windowpane	0	0	0	0	10.1	4.1	0	0	0	0
Hake	4.1	0.7	1.1	0.2	0.9	0.2	0	0	8.3	9.9
Winter flounder	0	0	0	0	6.4	3.9	0	0	0	0
Atlantic menhaden	5.7	2.3	0	0	0	0	0	0	0	0
Sea horse	0	0	0	0	0	0	0	0	14.6	0.7
Atlantic cod	0	0	0	0	0	0	3.3	13.5	0	0
Fourspot flounder	0	0	0	0	1.8	0.9	0	0	0	0
American plaice	0.8	0.1	1.1	<0.05	0	0	0	0	0	0
Wrymouth	0	0	0	0	1.8	0.9	0	0	0	0
Pollock	0.8	0.4	0	0	0	0	0	0	0	0
Filefish	0	0	0	0	0	0	0	0	2.1	0.5
Halfbeak	0	0	0	0	0	0	0.5	0.1	0	0
Longhorn sculpin	0	0	0	0	0	0	0	0	0	0
Unidentified fish	4.9	<0.05	3.2	<0.05	2.8	0.1	8.7	0.1	12.5	2.9
Spiny dogfish	0	0	10.8	3.7	2.8	16.6	0	0	0	0
Skate	0	0	0	0	9.2	9.3	0.5	0.3	0	0
Skate egg case	0	0	1.1	<0.05	1.8	<0.05	0	0	0	0
Squid	48.8	1.8	14.0	0.5	35.8	1.8	22.4	2.5	60.4	12.9
Octopus	0	0	0	0	0	0	0	0	2.1	0.5
Shrimp	0	0	0	0	0	0	2.7	<0.05	0	0
Lobster	0	0	0	0	1.8	0.5	0	0	0	0
Argonaut	0	0	0	0	0	0	0	0	4.2	0.4
Crab	0	0	0	0	0.9	<0.05	0.5	<0.05	0	0
Salp	0	0	0	0	1.8	0.1	0	0	0	0
Fig sponge	0	0	0	0	27.5	27.2	0	0	0	0
Finger sponge	0	0	0	0	0	0	0.5	<0.05	0	0

relation ($P<0.001$) between prey and bluefin tuna lengths was found for all prey-size data (Fig. 5). Despite this correlation, there appeared to be little association between predator and prey length for most species. The positive correlation was influenced by 29 larger prey items (>40 cm) all consumed by bluefin tuna larger than 230 cm. The larger prey were spiny dogfish, skate, bluefish, or Atlantic cod. Size data on the four most common prey species provided evidence of the consistency of prey size across a wide range of bluefin lengths in the Gulf of Maine. A significant positive size relationship was found for sand lance and Atlantic mackerel (both $P<0.001$), although both may have contained biases. The relationship for sand lance was influenced by smaller bluefin tuna that ate smaller sand lance (t-test, $P<0.001$) in Great South Channel than at Stellwagen Bank. All mackerel were YOY or age-1, except for two large mackerel consumed by larger bluefin tuna (>200 cm). The predator-prey size relationships for Atlantic herring ($P=0.36$) and squid ($P=0.16$) were not significant. A large majority (93%) of Atlantic herring prey were 18–27 cm in length, which corresponds to age-2 to age-4 cohorts for the western Gulf of Maine (Penttila et

Table 4

Summary statistics on stomach-contents biomass (g wet weight) from bluefin tuna caught at five seasonal feeding areas off New England, 1988–92. The geometric mean, confidence intervals (CI), and coefficient of variation (CV) are backtransformed from natural logarithms.

Statistic	All areas	Jeffreys Ledge	Stellwagen Bank	Cape Cod Bay	Great South Channel	South of Martha's Vineyard
Number of stomach samples with prey	568	123	93	109	183	48
Minimum stomach biomass	5	5	5	5	5	5
Maximum stomach biomass	16100	5800	6240	2900	16100	1200
Arithmetic mean	999	1957	1012	389	925	124
Geometric mean	214	832	438	133	126	37
Lower 95% CI	180	608	324	96	91	23
Upper 95% CI	255	1140	593	184	174	60
CV	39	26	24	35	46	44

al., 1989), and the youngest were age 2. There were no young-of-the-year (YOY) sand lance. Most sand lance from Great South Channel samples were age 2, in contrast to age 3 or age 4 at Stellwagen Bank (Weston et al., 1979). Most squid were YOY or age 1.

Numbers of prey species Few prey species were found in large numbers in a given stomach sample. Only sand lance, squid, Atlantic herring, and Atlantic mackerel had sample counts higher than 20 individual fish (Table 6). Data on prey numbers are limited because prey counts were made for only 208 samples. Many samples with large numbers of well-digested sand lance were difficult to count. From this subsample, the mean number of sand lance per stomach was 159, much higher than the next highest mean of 19 for Atlantic herring. Squid and mackerel commonly occurred as prey, although typically only a few individuals were found per stomach.

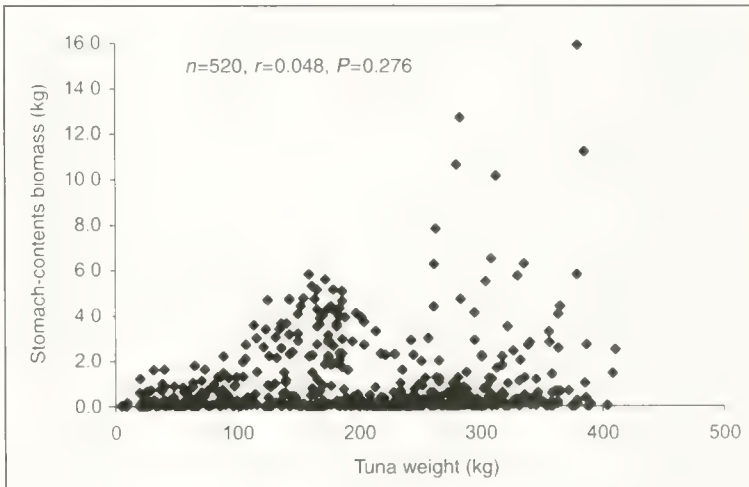

Figure 3

Scatterplot of bluefin tuna stomach-contents biomass and bluefin tuna weight for all samples from the Gulf of Maine, 1988–92.

Weight of prey species Sand lance and Atlantic herring (combined) accounted for 75% of the total stomach-contents biomass for all areas combined. The next highest species was bluefish at 7%. Despite a high frequency of occurrence, squid accounted a low percentage of overall biomass (2%) and a mean stomach prey weight of only 58 g. The highest mean prey weight was 1794 g for Atlantic herring. Only three other prey items averaged over 500 g in stomach-content weight: spiny dogfish (807 g), bluefish (742 g), and sand lance (661 g). With few exceptions, stomachs that were full or near full, contained only sand lance or Atlantic herring. Only five stomachs contained over 10 kg of prey contents: three with Atlantic herring, and one each with sand lance and Atlantic cod (16.0 kg, the largest meal observed).

In summary, five prey items occurred in frequency and mass to be considered important dietary components of the stomach contents sampled: sand lance, Atlantic herring, squid, Atlantic mackerel, and bluefish. Of these prey items, sand lance and Atlantic herring were the primary contributors to the diet of bluefin tuna sampled.

Discussion

Comparison of this study with previous west Atlantic bluefin tuna food habit studies revealed that fish prey represented a large majority of the diet, and cephalopods (primarily squid) were important secondary prey. Other prey taxa were minor components of the diet, except for Salpidae (Mason, 1976; Eggleston and Bochenek, 1990) and Amphipoda (Dragovich, 1970) for juvenile bluefin tuna. Comparisons with the four studies in which bluefin

tuna were sampled prior to 1970 (Crane, 1936; Krumholz, 1959; Dragovich, 1970; Matthews et al.[1]) were limited because of small sample sizes. In pre-1970 studies, sand lance or benthic organisms were not found to be prey items. Mason (1976) was the first to record sand lance in bluefin stomach contents. In three later studies, sand lance were found to be the most frequently occurring prey, followed by squid (Holliday, 1978; Eggleston and Bochenek, 1990; and the present study).

Two limitations common to previous diet studies were the small number of samples collected and the broad geographical range over which they were collected. In contrast, large numbers of samples were collected in the present study, at discrete feeding grounds on the New England continental shelf; moreover this study is the first in which the diet of bluefin tuna in the Gulf of Maine was quantified during their seasonal feeding migration. The major contribution of Atlantic herring and the common occurrence of demersal organisms as prey have not been previously recorded for bluefin tuna in the western North Atlantic Ocean.

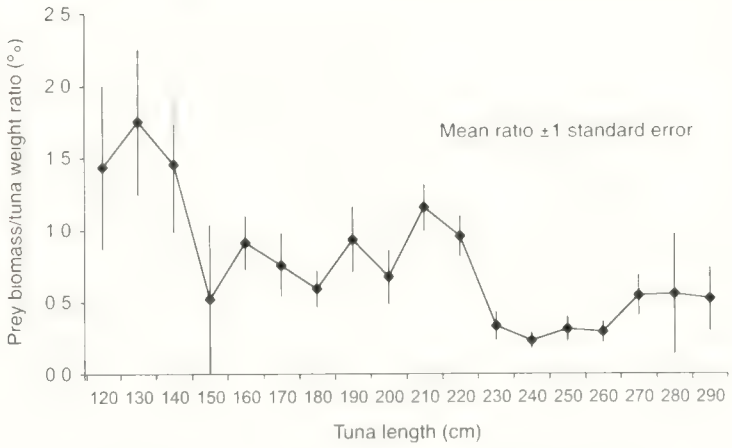

Figure 4

Relationship between the ratio of stomach-contents biomass to tuna weight (% wet weight [kg/kg]) and tuna length (curved fork length). All Gulf of Maine samples for bluefin lengths of 120–299 cm (n=519) were combined and arranged in 10-cm bins.

Sampling biases

Regurgitation, diel and seasonal effects, differential digestion rates, postcapture digestion, and predator size effects can be problematic to food habit studies and can bias data collection. (Bowen, 1986). This section discusses the potential effect that sampling biases may have on the findings of significant differences in the stomach-contents biomass and prey associations. A majority of the empty stomachs had distended stomach rugae, indicating that regurgitation had occurred. Similar observations were made during previous studies (Mason, 1976; and Dragovich, 1970), which would cause a negative bias for stomach-contents weight measurements. Diel and seasonal effects on feeding are difficult to assess and are large sources of variation. Large intersample variance can be expected given the complex interactions between predator populations and the temporal and spatial distribution of prey (Smagula and Adelman, 1982; Hodgson et al., 1989). Increasing sample size often may reduce variability, but high intra-

Table 5

Summary statistics for length data from major prey items in stomach contents and bluefin tuna sampled from Gulf of Maine (GOM), July–October, 1988–92. Prey lengths are total length, except for squid, which are mantle lengths. Bluefin tuna lengths are curved fork length (CFL). Area 1 = Jeffreys Ledge; area 2 = Stellwagen Bank; and area 4 = Great South Channel. n = number of samples taken.

		Prey				Bluefin tuna			
Species	Area	n	Mean (cm)	SD (cm)	Range (cm)	n	Mean (cm)	SD (cm)	Range (cm)
All prey	GOM	1866	17.7	7.27	3–80	190	220	38.60	104–297
Atlantic mackerel	GOM	150	15.9	3.27	10–36	40	215	42.56	132–272
Squid	GOM	89	13.8	5.63	3–24	41	224	30.81	159–295
Atlantic herring	GOM	364	24.6	2.51	18–31	57	211	30.19	119–276
Atlantic herring	1	263	24.4	2.65	18–31	42	209	27.83	119–276
Atlantic herring	4	91	25.1	1.94	21–30	9	221	42.05	130–272
Sand lance	GOM	1176	14.9	3.04	8–23	41	206	45.51	124–279
Sand lance	2	468	17.2	2.27	12–23	16	232	30.27	178–269
Sand lance	4	609	12.8	1.48	8–19	21	186	44.99	124–279

sample and intersample variation, prey weight skewness, and variance dependency are widespread findings in food habit studies that reflect natural feeding interactions (Smagula and Adelman, 1982; Amundsen and Klemetson, 1986; and Hodgson et al., 1989). Large sample variation was evident in the present study and limited the application of parametric statistics.

Differential digestion rates can result in an underestimate of the relative importance of a major prey item (Hyslop, 1980). Soft-bodied squid likely undergo digestion quicker than bony fish, and, therefore, prey weight measurements may have been negatively biased. Postcapture decomposition of prey has not been measured for bluefin tuna but may negatively bias stomach-contents weight for samples held a long time after capture (Holliday, 1978). The effect of bias on the prey weight data is suspected to be minor because of strong market incentives to chill harvested bluefin tuna and because samples were collected soon after capture.

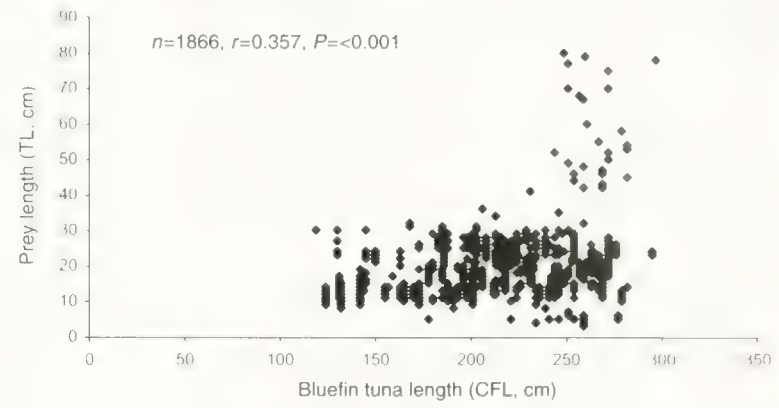

Figure 5

Relationship between bluefin tuna length and prey length for all Gulf of Maine samples during 1988–92 that contained measurable prey (190 stomach samples).

The separation of chum bait from natural prey and the exclusion of chum from diet analyses were potential minimal sources of bias. Because bluefin tuna swallow prey whole and chum is cut into small pieces, cut chum was readily separated from natural prey in stomach samples. Samples of small bluefin tuna that fed on the discards of trawlers in the area south of Martha's Vineyard did present a problem, and many of these samples were removed from analyses because natural prey and discards could not be distinguished. Other study areas did not indicate an association between tuna fisheries and trawl fishing; consequently, no evidence of discard feeding was observed. It is possible that the availability of chum could limit feeding on natural prey, although no evidence of this was found. Most chum was observed in the stomach contents of bluefin tuna from Stellwagen Bank and Jeffreys Ledge, but these areas also had the highest mean stomach-contents biomass and lowest frequency of empty stomachs.

Most of these biases were negative, possibly decreasing prey weight measurements in stomach contents, and could not easily be separated from natural conditions that lead to suboptimal feeding habits. Butler and Mason (1978) re-

Table 6

Prey number and prey weight data for the most common prey in stomach contents of bluefin tuna caught off New England during 1988–92. Both number of prey and prey weight were derived from all samples with prey (n=568), but prey number only includes samples where all prey could be counted.

	Number of prey			Prey weight (g)		
Prey species	n	Mean	Range	n	Mean	Range
Sand lance	25	159	2–557	194	661	5–10,590
Squid	76	3	1–28	186	58	5–1440
Atlantic herring	85	19	1–84	167	1794	5–12,700
Atlantic mackerel	27	6	1–30	108	175	5–1210
Bluefish	22	1	1 2	55	742	5–5800
Fig sponge	19	3	1–10	30	384	5–1250
Butterfish	10	2	1–5	21	80	5–450
Silver hake	1	17		16	93	5–250
Spiny dogfish	3	2	1–4	13	807	5–2900
Skate	9	1	1–2	13	359	50–810
Windowpane	11	1	1–3	12	158	40–250
Hake	5	2	1–3	11	227	40–640

ported higher daily consumption rates for pen-held bluefin tuna, an average of 28 kg per day during single feedings to satiation, and 40 kg per day during multiple feedings. Data from my study implied that naturally feeding bluefin tuna do not often reach these consumption rates: only five of 568 stomachs had prey contents over 10 kg. Regurgitation is a major confounding factor for stomach-contents biomass data and presents a serious challenge for calculations of daily rations and bioenergetic modeling of bluefin tuna feeding habits. The anatomy of the alimentary canal, combined with the stress of capture, appears to cause a high rate of regurgitation.

Cape Cod Bay

The bluefin tuna prey composition from Cape Cod Bay was unlike any prey composition previously reported for the west Atlantic, in that no individual prey item dominated nor was encountered at a high frequency of occurrence or percentage of stomach-contents biomass. In previous west Atlantic bluefin tuna food-habit studies, prey composition was dominated by a single, pelagic, schooling prey species (followed by a few secondary species of much less importance), and Pinkas (1971) reported similar results for Pacific bluefin tuna. Finding fig sponge as the highest ranked prey item in the diet of bluefin tuna in Cape Cod Bay was surprising; sessile prey organisms had not been found in previous bluefin tuna food-habit studies. Occurrence of fig sponge, locally known as "monkey dung," in the stomachs of bluefin tuna is commonly known to Cape Cod Bay fishermen who have questioned whether it is natural prey or whether it is accidentally swallowed during capture. I found the sponge at various stages of digestion; well-digested pieces as well as fresh pieces were found in the same stomach. The differential stages of digestion implies that fig sponge was ingested either as selected prey of unknown attraction and nutritional value or as incidental catch to a targeted bottom dweller.

Bottom foraging in the relatively shallow Cape Cod Bay (average depth: 25 m) was evident because eight of the 16 prey items identified were benthic or demersal species. Vertical excursions to the bottom in shallow regions were not unexpected, yet bottom foraging has not been reported for west Atlantic bluefin tuna. Bottom feeding was evident for most locations in this study, including foraging on small crabs (*Cancer* spp.) and finger sponge at Great South Channel where depths approached 100 m. In Cape Cod Bay, bottom foraging may not be the optimal feeding strategy for bluefin tuna and may simply be a response to low food availability, as suggested by the low prey biomass and higher proportion of naturally empty stomachs.

Prey size

To date, prey size in bluefin tuna food habit studies in the western North Atlantic has received little attention. Only Matthews et al.[1]) presented prey size data, a mean value based on 38 bluefin tuna stomachs. Young et al. (1997) found no relationship between prey size and size (40–192 cm) of juvenile southern Atlantic bluefin tuna (*Thunnus maccoyii*). I found only minor evidence of a predator-prey size relationship for bluefin tuna in the Gulf of Maine. A positive correlation was found between sand lance and bluefin length, although regional differences in the lengths of both species appears to bias the correlation. Smaller sand lance and bluefin tuna were found at Great South Channel than at Stellwagen Bank. A positive interaction between bluefin tuna and prey sizes was indicated by the consumption of the largest prey (>40 cm) by large bluefin tuna (>230 cm). Prey this large were not common in stomachs and were probably limited by mouth and esophagus gape. Otherwise, the sizes of prey were consistent across the range of bluefin tuna sampled in the Gulf of Maine.

The findings on prey size and numbers (per stomach) provide evidence of three selective foraging strategies used by bluefin tuna in the Gulf of Maine. Feeding on individual, fast-swimming pelagic prey was evident from consumed bluefish and Atlantic mackerel that are abundant pelagic species in the Gulf of Maine, but which occurred much less frequently in stomach contents and with few individuals per stomach. Ram feeding (swimming through a dense school prey with mouth open) of small prey may have resulted in high average number of sand lance found in stomachs and contributed to the similar prey sizes in most sizes of bluefin tuna. Bluefin tuna in Cape Cod Bay displayed a different foraging behavior, selecting larger, individual demersal prey. The variation in prey composition and different feeding strategies is consistent with previous descriptions of bluefin tuna as an opportunistic predator. However, the dominance of sand lance and Atlantic herring in the Gulf of Maine diet suggests a dependence on these species as an optimal energy source.

Trophic influences on bluefin tuna distribution

Changes in biomass and spatial availability of forage populations may affect the distribution of bluefin tuna on the New England continental shelf. Major changes in the prey community of the Gulf of Maine have occurred in recent decades. After Atlantic mackerel and Atlantic herring stocks off New England were severely overharvested in the 1960s and 1970s (NOAA, 1998), sand lance populations increased, presumably as a result of decreased predation and competition for food (Sherman et al., 1981). Atlantic herring and Atlantic mackerel stocks off New England increased steadily during the 1980s and 1990s (NEFSC, 1998). By the mid-1990s, the U.S. Atlantic coastal spawning stock biomass for these species increased to the highest levels on record (NEFSC, 1998).

Commercial bluefin tuna catches have increased in areas where Atlantic herring abundance has increased (western Gulf of Maine and Great South Channel) and diminished at traditional areas south of the Gulf of Maine (Chase, 1992). The northward shift in bluefin tuna distribution on the New England continental shelf may be influenced by improved foraging opportunities on Atlantic herring in the Gulf of Maine. I suspect that the timing of bluefin tuna migrations to the New England continental shelf are associated with seasonal spawning and feeding aggregations of Atlantic herring. Sand lance populations appear to be an important influence on bluefin tuna feeding migrations,

but they occur on a limited spatial scale in relation to Atlantic herring in the Gulf of Maine, and changes in their population abundance are not well documented. Atlantic herring and sand lance are also important in the diet and distribution of marine mammals in the Gulf of Maine (Payne et al., 1990; Weinrich et al., 1997; Gannon et al., 1998).

Changes in bluefin tuna stock composition and the long-term impact of small-mesh trawling gear on commercially important prey items (squid, silver hake, and butterfish) in southern New England waters and Mid-Atlantic areas where bluefin tuna catches have diminished are two potentially confounding factors in this discussion. In the management of Atlantic bluefin tuna, care should be taken to recognize that the fluctuations in the regional abundance of this species can be influenced by more than changes in stock structure. Changes in major prey populations, produced either by environmental features or by fishery practices, can have a profound effect on regional aggregations of bluefin tuna. Investigations should be conducted on introducing forage-base information into the interpretation of catch-per-unit-of-effort indices of abundance for Atlantic bluefin tuna populations. There is also a need for future research to improve our knowledge on the bioenergetics of this warm-bodied tuna and its associated relationships with prey species.

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Movement of American lobster (*Homarus americanus*) in the southwestern Gulf of St. Lawrence

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Abstract—A total of 42,445 American lobsters (*Homarus americanus*) were tagged in thirty-one sites throughout the southwestern Gulf of St. Lawrence between 1980 and 1997. Results from the recapture of 8503 tagged lobsters showed small distances traveled between the release and the recapture position for animals ranging in size from 51 to 152 mm carapace length. The average distance traveled ranged from 2 km in parts of Baie des Chaleurs and western Cape Breton to 19 km in central Northumberland Strait. Lobsters moved generally along the shore (93% of the dispersion was in areas between the shore and the 20-m bathymetric contour). As a result, lobsters traveled longer distances in sites characterized by a gradually sloping bottom where the distance between the shore and the 20-m contour line was extensive in contrast to areas characterized by rapidly changing depths and by a relatively small amount of habitat shallower than 20 m. In the majority of sites (14 of 19) there was no significant difference between males and females in the average distance they traveled. In four of the five sites females moved farther than males. In general, the average distance traveled by berried females was shorter than that traveled by males or nonberried females. No relationship was observed between the distance traveled and the size of the animal. There was no strong evidence of a relationship between the average distance traveled and the number of days at liberty. In general, lobsters in the southwestern Gulf of St. Lawrence traveled short distances and dispersion was restricted to the nearshore habitat. Further, the distance traveled was not correlated to size, sex, or years at large. These findings show that there is little interaction between American lobsters from different fishing areas at the benthic level and that American lobster movements should have minimal consequences for management of the species in the southwestern Gulf of St. Lawrence.

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The American lobster (*Homarus americanus* Milne-Edwards, 1837) fishery in the southwestern Gulf of St. Lawrence (GSL) and for the entire Canadian Maritime Provinces has become the most economically important fishery of coastal communities. Consequently, there is increasing interest by fishermen and the fishing industry to better understand the biology of the species and factors that may play a role in the fluctuations of landings, including possible lobster movements between lobster fishing areas (LFAs). Fishermen are particularly concerned by lobster movements because the minimal legal size increased in different LFAs in the southwestern GSL throughout the 1980s and 1990s, and they want to know whether lobsters returned at sea in a given area could be recaptured elsewhere.

Several tagging projects have been conducted in the past to study lobster movements in the GSL (Table 1). These tagging projects, initiated in the 1930s by Templeman (1935), showed that the average distance traveled by lobsters in the GSL was generally less than 15 km and that very few animals traveled up to 70 km (for review see Stasko, 1980; Lawton and Lavalli, 1995). Other tagging studies conducted in inshore waters outside the GSL in Nova Scotia (Wilder, 1974; Campbell, 1982, 1989; Campbell and Stasko, 1985; Miller et al., 1989; Tremblay et al., 1998), Bay of Fundy (Campbell, 1986; Campbell and Stasko, 1986), Maine (Cooper, 1970; Cooper et al., 1975; Krouse, 1981), New Hampshire (Watson et al., 1999), Massachusetts (Karnofsky et al., 1989) and Rhode Island (Fogarty et al., 1980) have also shown that lobster movements were generally similar (4 to 18 km) to those from the GSL. However, long-distance movements of more than 90 km for up to 20% of the animals have also been observed for lobsters tagged inshore (Dow, 1974; Fogarty et al., 1980; Campbell and Stasko, 1985, 1986; Campbell, 1989; Robichaud and Lawton, 1997); the farthest distance traveled reported was 798 km (Campbell and Stasko, 1986). These long distances traveled are more similar to those reported for offshore lobsters tagged on the continental shelf and over the offshore deep canyons (Saila and Flowers, 1968; Cooper and Uzmann, 1971; Uzmann et al., 1977; Fogarty et al., 1980; Campbell et al., 1984; Campbell and Stasko, 1985). Movements of more than 70 km have never been reported for lobsters tagged in the southwestern GSL.

Since 1980, forty-six tagging studies have been conducted throughout the southwestern GSL, mostly in areas where information on lobster movements has been unavailable. These tagging studies have covered fishing grounds characterized by a flat bottom and having a relatively smooth transition from shore to 30 m and a narrow habitat close to shore where changes in depths occur over a relatively short distance. The purpose of our study was to investigate the benthic movement of lobsters tagged in different locations within the southwestern GSL by comparing the distance traveled, number of days at liberty, and size and sex of lobsters.

Materials and methods

The recapture position was documented for 8503 lobsters, ranging in size from 51 to 152 mm carapace length (CL), from a total of 42,445 tagged and released during forty-six tagging studies in thirty-one sites throughout the southwestern GSL (Fig. 1) between 1980 and 1997 (Table 2). The animals were captured by traps and tagged between July and November after the commercial fishing seasons (May and June in LFAs 23, 24, 26A, and 26B, and from mid-August to mid-October in LFA 25). The CL, measured to the nearest mm, sex of each animal, and presence or absence of eggs under the female abdomen were recorded. Prior to 1989, all animals were tagged with orange sphyrion anchor tags, and blue streamer tags were used after 1992. Between 1989 and 1992 inclusively, both type of tags were used. A description of the tags and the tagging technique are presented in Moriyasu et al. (1995) and Comeau et al. (1998).

The positions of recaptured lobsters came from fishermen. Because all tagging projects were undertaken after each commercial fishing season, no lobsters were recaptured during the same year of their tagging. To increase fishermen's participation in reporting tagged animals, a major awareness campaign was conducted. Prior to 1993, representatives of the Department of Fisheries and Oceans (DFO) were present at each wharf to measure and collect information on tagged lobsters that were recaptured. Beginning in 1993, letters were sent to all lobster fishermen in regions where tagging projects were conducted; in these letters the tagging project was described, in-

Table 1

Locations and authors of lobster tagging studies on movements of American lobster (*Homarus americanus*) conducted in the Gulf of St. Lawrence.

Location	Authors and date
Various locations in Gulf of St. Lawrence	Wilder (1974)
West coast of Newfoundland	Templeman (1940)
Magdalen Islands (Québec)	Templeman (1935) Bergeron (1967) Munro and Therriault (1983)
Gaspé Peninsula (Québec)	Corrivault (1948)
Malpeque (Prince Edward Island)	Templeman (1935)
Western Prince Edward Island	Wilder (1963)
Northumberland Strait	Templeman (1935) Wilder (1963)

Figure 1

Locations (★) of American lobster (*Homarus americanus*) tagging studies conducted in the southwestern Gulf of St. Lawrence between 1980 and 1997. The names of each site are presented in Table 2. The lobster fishing areas (LFAs) are indicated on the map.

structions given for returning lobster tag information, and the cooperation of the fishermen was sought (Comeau et al., 1998). Similar information was posted at wharves. For each tagged lobster, fishermen were asked to record date of capture, tag number, position of capture, and depth. They were then asked to freeze the animal with the tag still attached and contact an information collection center, where they could leave their names, addresses, and telephone numbers. A DFO representative collected tagged lobsters for measurement and reimbursed fishermen according to the market value of the recovered lobsters. No reward was issued. Fishermen also had the option to bring the lobsters and the information to a fisherman-representative. If a tagged lobster under the legal size or a tagged berried female was captured, fishermen were asked to record the above information and release the lobster to the water with the tag still attached.

The distance traveled by each recaptured animal was calculated as the linear distance between release and recapture positions. The Kruskal-Wallis and Mann-Whitney (*U*-test) tests were used to compare the average distance traveled for males, females, and berried females for ani-

Table 2

Average distances traveled by American lobsters tagged in the southwestern Gulf of St. Lawrence between 1980 and 1997. The number of each site corresponds to its geographical position on the map in Figure 1. n = number of recaptured lobster with tags indicating release location for which distance traveled to recapture site could be calculated.

Tagging site	Year of tagging	n	Average carapace length ±SD (mm)	Carapace length range (mm)	Average distance traveled ±SD (km)
1 Belledune	1980	604	70.5 ±4.9	50–115	7.4 ±6.5
2 Pointe-Verte	1996	26	78.2 ±6.4	71–90	6.1 ±4.0
3 Stonehaven	1994–97	618	73.2 ±5.4	53–111	2.4 ±3.0
4 Anse-Bleue	1994	290	73.5 ±4.8	54–91	3.5 ±6.3
5 Caraquet	1993–97	1416	74.2 ±9.2	55–133	8.0 ±8.8
6 Petit-Shippagan	1994	134	76.2 ±10.4	54–116	8.7 ±8.8
7 Miscou	1995	58	69.9 ±8.2	66–117	4.5 ±6.5
8 Le Goulet	1996	101	73.8 ±6.2	59–98	5.3 ±3.5
9 Val Comeau	1985, 1996–97	519	76.3 ±9.1	57–117	7.0 ±6.5
10 Néguac	1996	74	78.0 ±8.7	65–105	14.2 ±8.2
11 Escuminac	1997	17	73.9 ±5.2	66–88	9.6 ±9.9
12 Seacow Pond	1996	62	71.1 ±6.0	61–94	5.3 ±7.8
13 Alberton	1996	62	74.0 ±6.9	65–97	5.7 ±5.9
14 Malpeque	1989	492	68.1 ±7.2	51–100	10.1 ±7.0
15 Tracadie	1984	27	68.1 ±12.4	55–111	10.4 ±10.1
16 North Lake	1996	78	72.8 ±5.0	61–89	2.5 ±3.4
17 Pointe-Sapin	1996	22	72.5 ±5.0	65–83	6.7 ±4.1
18 Kouchibouguac	1997	53	67.7 ±4.3	60–74	8.0 ±7.3
19 Cap-Pelé	1997	41	72.2 ±6.0	60–84	12.2 ±11.9
20 Skinner's Pond	1996	13	71.4 ±5.8	63–131	5.4 ±6.7
21 Miminegash	1996	37	74.1 ±8.5	64–100	8.6 ±10.8
22 Howard's Cove	1995	79	66.9 ±7.1	54–84	15.3 ±13.2
23 Egmont Bay	1982	15	66.1 ±7.0	58–77	19.4 ±16.0
24 Souris	1996	213	75.4 ±7.1	59–109	4.9 ±6.8
25 Fortune	1996	208	72.7 ±3.9	66–84	3.3 ±3.6
26 Beach Point	1982	243	88.0 ±12.9	61–120	7.4 ±8.9
27 Lismore	1997	51	78.2 ±11.4	58–103	7.8 ±12.4
28 Ballantynes Cove	1986	226	74.0 ±11.2	55–130	9.3 ±13.0
29 Port Hood	1988	339	67.4 ±11.6	51–150	4.5 ±2.9
30 Margaree	1984, 1988, 1992	1332	70.7 ±8.5	52–152	3.2 ±5.1
31 Pleasant Bay	1988, 1992	1053	69.8 ±8.1	54–130	2.3 ±2.1

mals recovered during the first recapture period following their tagging. Correlation (r) was used to determine the relationship between the distance traveled and the size of the animal. To determine the relation between the average distance traveled and days at liberty, sites with recaptures over multiple years were used. The relationship between the average distance traveled and the extent of shallow waters was also established. The extent of shallow waters was quantified as the distance from shore to the closest 30-m bathymetric contour for each tagging site.

Results

A total of 7565 tagged lobsters were returned during their first recovery period, with size and geographical position at recapture. Only sites with fifty recaptures or more were considered. There was no evidence of a relationship between the size of the animal and distance traveled in the southwestern GSL because the correlation coefficient (r) ranged from –0.19 to 0.23 (Table 3). In this study, small lobsters (<70 mm CL) traveled as far as the large animals (>90 mm CL) (Fig. 2).

Table 3

Correlation coefficient (r) for the relationship of the distance traveled and the carapace length (CL) of American lobsters tagged in the southwestern Gulf of St. Lawrence. The number of each site corresponds to its geographical position on the map in Figure 1. n = number of recaptured lobster with tags indicating release location for which distance traveled to recapture site could be calculated.

Tagging site	n	CL range (mm)	r
1 Belledune	536	50–115	–0.12
3 Stonehaven	580	53–111	0.04
4 Anse-Bleue	232	54–91	0.02
5 Caraquet	1288	55–133	0.08
6 Petit-Shippagan	117	54–116	0.10
8 Le Goulet	90	59–98	–0.03
9 Val Comeau	500	57–117	–0.05
10 Neguac	72	65–105	0.22
12 Seacow Pond	61	61–94	0.08
13 Alberton	61	65–97	–0.08
14 Malpeque	251	51–100	0.11
16 North Lake	64	61–89	0.18
18 Kouchibouguac	51	60–74	–0.06
22 Howard's Cove	73	54–84	–0.19
24 Souris	202	59–109	0.14
25 Fortune	207	66–84	0.04
26 Beach Point	243	61–120	–0.02
27 Lismore	51	58–103	0.13
28 Ballantynes Cove	188	55–130	0.23
29 Port Hood	339	51–150	0.20
30 Margaree	1319	52–152	–0.05
31 Pleasant Bay	1040	54–130	0.04

There was no significant difference in the average distance traveled between males and females in eleven out of nineteen sites (Table 4). Females traveled significantly farther than males (Table 4) at three sites located in the upper part of Baie des Chaleurs (Fig. 1, sites 1, 3, and 4) and one site on the northeastern tip of Prince Edward Island (Fig. 1, site 25). The only site where males traveled significantly farther than females was in Val Comeau (Table 4, Fig. 1, site 9). No significant differences were observed in the average distance traveled by berried females compared with males or nonberried females in four out of nine sites where data were available for berried females (Table 4). The average distance traveled by berried females was significantly shorter than that by both males and females in three sites (Table 4, sites 9, 16, and 25) and significantly farther only in Port Hood (Table 4, site 29). In Souris (Table 4, site 24), no significant difference was observed for average distance traveled between males and berried females, but they were both significantly shorter than the average distance traveled for nonberried females.

Only seven out of thirty-one sites had a sufficient number of recaptures over multiple years to allow a comparison between distance traveled and days at liberty. A substantial decrease in the percentage of tags recaptured from the first to the second and third recovery periods was observed (Table 5), reflecting high exploitation rates by the fishery. There is no strong evidence of a positive relationship between the average distance traveled and days at liberty. No significant difference (P>0.05) was observed in the average distance traveled over time in Stonehaven (site 3), Anse-Bleue (site 4), Caraquet (site 5) and North Lake (site 16) (Table 5). The average distance traveled decreased significantly (P=0.0002) in Belledune (site 1), whereas it increased significantly in Souris (site 24) (P=0.0119) and Margaree (site 30) (P=0.004) over multiple years recovery (Table 5). Even in these areas where distances were significantly different, the differences were not large (2.4, 2.3, and 5.3 km). Also, the longest distance traveled observed for the second or third (or both) recovery periods was equal or less than the one observed for the first recovery period for all 7 sites (Table 5).

Lobster movements in the southwestern GSL seemed to be restricted to short distances along the coast near shore in areas where the lobster habitat is restricted to a few kilometers from the shore and longer distances over a broader gradually sloping bottom (Fig. 3). In general, 93% of lobster dispersions were limited to the 20-m bathymetry contour. The shorter average distances traveled (2.4–4.9 km, Table 2) were observed in part of Baie des Chaleurs (Figs 1 and 4, sites 3 and 4), the northeastern tip of Prince Edward Island (Fig. 1, sites 16, 24, and 25) and Cape Breton (Figs 1 and 5, sites 29, 30, and 31). Relatively short average distances (5.3–8.6 km, Table 2) were observed around northeastern New Brunswick (Figs 1 and 6, sites 1, 2, 5, 6, 8, and 9), the northwestern tip of Prince Edward Island (Fig. 1, sites 12, 13, 20, and 21), eastern New Brunswick (Fig. 1, sites 17 and 18) and the eastern end of

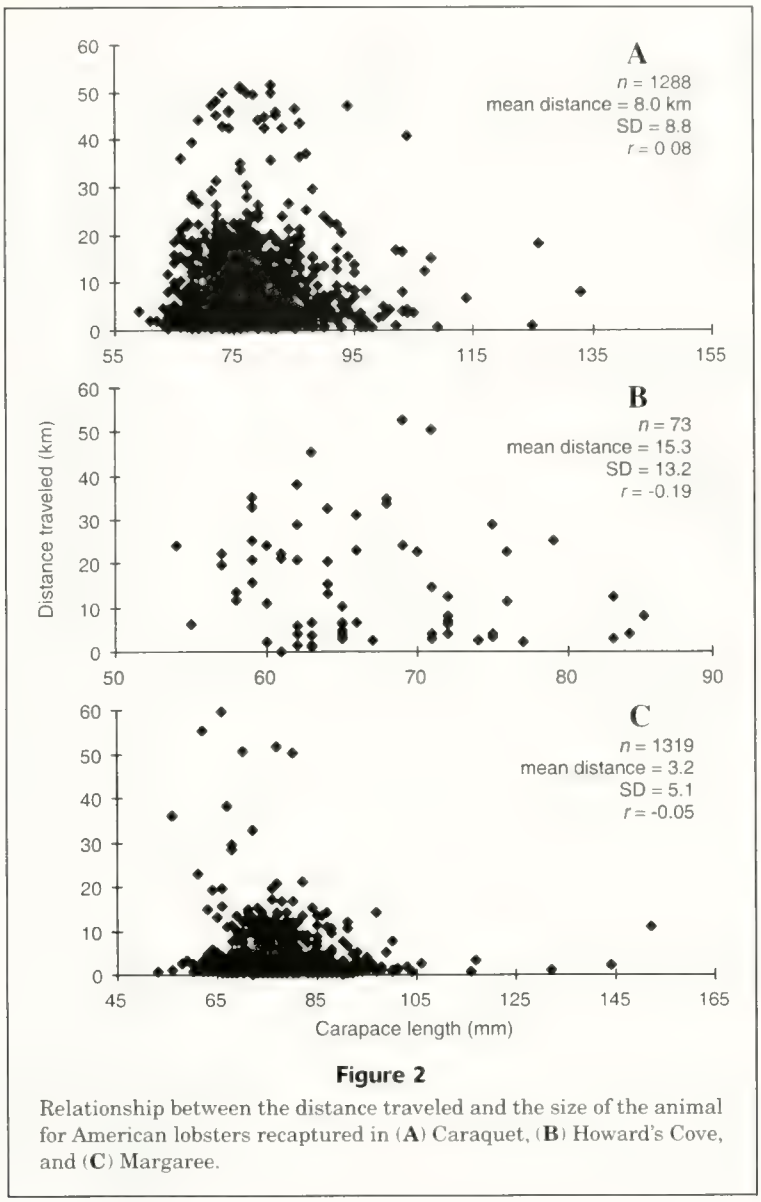

Figure 2

Relationship between the distance traveled and the size of the animal for American lobsters recaptured in (**A**) Caraquet, (**B**) Howard's Cove, and (**C**) Margaree.

the Northumberland Strait (Fig. 1, sites 26 and 27). The longest average distances traveled (9.3–19.4 km, Table 2) were observed in the immediate vicinity of Miramichi Bay (Figs 1 and 6, sites 10 and 11), Malpeque Bay and Tracadie Bay in northern Prince Edward Island (Fig 1, sites 14, and 15), St. Georges Bay (Fig. 1, site 28) and central Northumberland Strait (Figs 1 and 7, sites 19, 22, and 23).

Lobster movements in the Northumberland Strait were related to whether the site was located toward the center or at either extremity (either end) of the Strait. Lobsters at sites close to the external boundaries (Fig. 1, sites 17, 18, 20, 21, 26, and 27) traveled on average shorter distances (5.4–8.6 km) than those located in the center of the Strait (Fig. 1, 12.2–19.4 km, sites 19, 22, and 23). Although tags were recovered in the western portion of Northumberland Strait (LFA 25) at a different time (a different fishing season) compared with tag recoveries at the other LFAs, movements seemed to be related to the extent of shallow waters (<20 m) rather than the time of the recovery period.

Discussion

Lobster movements in the southwestern GSL are related to the local bottom topography and are depth-dependent, i.e. lobsters traveled on average longer distances in areas where the shallow waters (<20 m) extended farther from shore. We observed that on the narrow coastal shelf of western Cape Breton and in some areas in Baie des Chaleurs, lobsters traveled on average less than 5 km compared with distances ranging from 9.3 to 19.4 km in the gradually sloping bottom of the Northumberland Strait and some shallow bays. Similarly, Templeman (1935) reported

Table 4

Comparison of the average distance traveled between the average distance traveled by male, female, and berried female American lobsters. The number of each site corresponds to its geographical position on the map in Figure 1. *n* = number of recaptured lobster with tags indicating release location for which distance traveled to recapture site could be calculated.

Tagging site	Biological category	*n*	Average distance traveled ±SD (km)	*U*-Test or Kruskal-Wallis[1] *P*
1 Belledune	male	360	7.0 ±5.9	0.0003
	female	176	9.0 ±8.3	
3 Stonehaven	male	316	2.1 ±2.8	0.0248
	female	264	2.7 ±3.3	
4 Anse-Bleue	male	127	2.1 ±3.3	0.0056
	female	105	3.8 ±5.2	
5 Caraquet	male	746	8.1 ±9.1	0.0937
	female	487	7.7 ±8.6	
	berried female	55	5.5 ±6.6	
8 Le Goulet	male	45	5.3 ±2.7	0.4385
	female	45	5.2 ±2.7	
9 Val Comeau	male	279	7.7 ±7.1	0.0260[2]
	female	218	6.3 ±5.6	
	berried female	5	1.3 ±0.7	0.0018
12 Seacow Pond	male	20	5.0 ±7.7	0.5800
	female	41	5.5 ±7.9	
13 Alberton	male	33	6.0 ±6.7	0.8849
	female	29	5.4 ±5.0	
14 Malpeque	male	114	11.0 ±7.6	0.7310
	female	95	11.2 ±7.4	
	berried female	42	10.5 ±9.9	
16 North Lake	male	26	2.1 ±1.4	0.4700[2]
	female	33	3.5 ±4.9	
	berried female	5	0.8 ±0.6	0.0243
18 Kouchibouguac	male	25	8.9 ±7.8	0.5847
	female	26	8.0 ±7.0	
22 Howard's Cove	male	43	17.3 ±12.3	0.1333
	female	31	12.8 ±14.0	
24 Souris	male	131	3.6 ±5.3	0.5826[3]
	female	66	7.1 ±9.0	0.0140[2]
	berried female	5	1.6 ±0.7	0.0355
25 Fortune	male	133	3.2 ±3.6	0.0155[2]
	female	62	4.0 ±3.7	
	berried female	12	0.5 ±0.2	0.0001
26 Beach Point	male	178	6.4 ±6.2	0.4729
	female	65	10.1 ±13.4	
28 Ballantynes Cove	male	56	8.5 ±10.0	0.6193
	female	132	8.0 ±9.7	
29 Port Hood	male	139	4.4 ±3.1	0.7616[2]
	female	158	4.3 ±2.6	
	berried female	42	5.6 ±3.2	0.0294
30 Margaree	male	449	3.1 ±4.9	0.1478
	female	553	3.5 ±5.0	
	berried female	317	2.8 ±5.0	
31 Pleasant Bay	male	322	2.1 ±1.8	0.2638
	female	565	2.3 ±2.2	
	berried female	153	2.5 ±2.4	

[1] The *U*-test and the Kruskal-Wallis test were used to compare two and three groups, respectively.
[2] *U* test between males and females.
[3] *U*-test between males and berried females.

Table 5

The average and the longest distances traveled by American lobsters for sites with tags returned over multiple years. The time between tagging and recapture of the animal (number of days at liberty), and the number of observations (n) are indicated. The number of each site corresponds to its geographical position on the map in Figure 1.

Tagging site	Number of days at liberty	n	Average distance traveled (km)	U-test or Kruskal-Wallis[1] P	Longest distance traveled (km)
1 Belledune	295–378	497	7.6 ±6.1	0.0002	44
	678–747	72	6.7 ±7.5		37
	1048–1102	35	5.2 ±3.9		17
3 Stonehaven	231–291	580	2.4 ±3.0	0.5827	28
	598–648	38	2.4 ±4.1		17
4 Anse-Bleue	217–270	235	2.9 ±4.3	0.2753	32
	577–628	48	6.2 ±11.9		56
	942–972	7	5.0 ±7.3		17
5 Caraquet	213–360	1302	7.9 ±8.4	0.6416	51
	584–725	97	7.7 ±11.8		49
	965–1057	17	11.8 ±14.5		50
16 North Lake	232–280	65	2.7 ±3.7	0.2075	24
	605–641	13	1.7 ±1.5		6
24 Souris	230–285	202	4.7 ±6.9	0.0119	31
	584–625	11	7.0 ±4.2		13
30 Margaree	250–308	147	3.3 ±3.7	0.004	23
	622–671	13	8.6 ±7.6		21

[1] The U-test and the Kruskal-Wallis test were used to compare two and three groups, respectively

that the average distance traveled by lobsters from sites located on the north side of Prince Edward Island and the western part of the Northumberland Strait ranged from 7 to 10 km. As with our results, longer movements were reported in the Egmont Bay area (central Northumberland Strait); lobsters traveled an average distance of approximately 14 km (Wilder, 1963) on lobster habitat in shallow (<20 m) waters. In other sites within the GSL, lobsters also traveled on average small distances. Lobsters in the Magdelan Islands (Templeman, 1935; Bergeron, 1967) and on the northern shore of Baie des Chaleurs (Corrivault, 1948) traveled average distances ranging from 3 to 16 km and 12 km or less, respectively. On the west coast of Newfoundland, Templeman (1940) reported that lobsters traveled an average of 3.2 km in St. George's Bay and 8.2 km in Port-au-Port Bay; hence, lobsters disperse within the GSL, in general, over small distances in inshore waters.

Most of the lobster movements observed in the southwestern GSL were oriented along the coast in inshore waters. Although the shallow (<20 m) gradually sloping bottom of the central Northumberland Strait, the Malpeque Bay, and Miramichi Bay areas allows for longer and more broader dispersions, lobsters remain close to either the New Brunswick, Nova Scotia, or Prince.Edward Island coastline, or confined to a bay environment. However, dispersions along the coast might not be the only types of lobster movements in southwestern GSL. Movements perpendicular to the coast have been documented in the Magdalen Islands (Templeman, 1936; Bergeron, 1967; Munro and Therriault, 1983), Bonavista Bay in Newfoundland (Ennis, 1984), and on the north shore of Baie des Chaleurs (Corrivault, 1948) because a migration of lobsters moving inshore in the spring and offshore in the fall was observed.

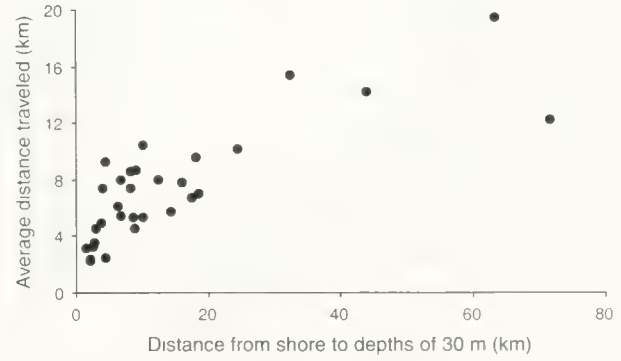

Figure 3

Relationship between the average distance traveled and the extent of shallow waters measured by the distance from shore to the closest 30-m bathymetric contour.

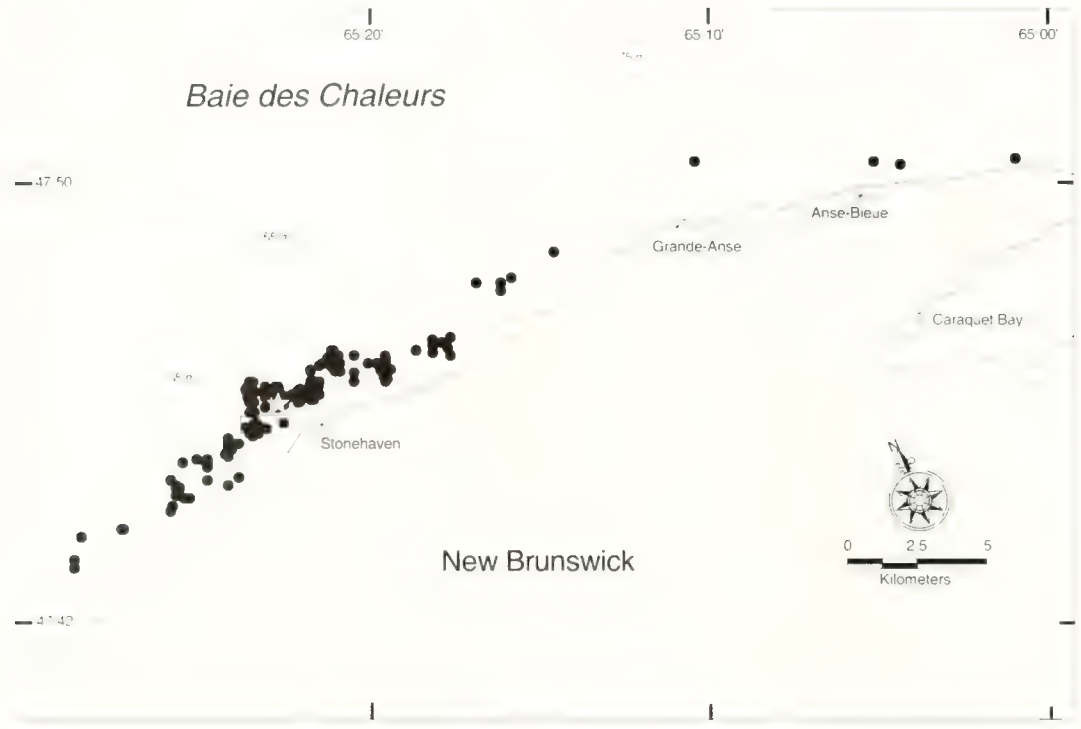

Figure 4

Locations (•) of tagged American lobsters recaptured in 1995 and 1996 (n=296) from the 1994 tagging project conducted in Stonehaven, New Brunswick. The release sites are indicated by a star symbol.

Recently, a trawl survey conducted at a depth of 40 m in the Caraquet area (Baie des Chaleurs) over a 7-month period produced lobsters in mid-May, late-October, and November, but not between June and early-October (Comeau, personal obs.). Further, the recapture positions during the fishing season showed that lobsters tagged during these trawl surveys were recaptured along the coast at depths less than 20 m from Stonehaven to Miscou (Comeau, personal obs.). This finding suggests that there is an inshore–offshore movement on the south shore of Baie des Chaleurs similar to the one observed by Corrivault (1948) on the north shore of that bay. Unfortunately, our tagging projects were not designed to study this type of movement and did not allow us to speculate more on inshore–offshore movements.

The lack of long-range movements across the southwestern GSL could be explained by the presence of an extensive cold (<1.5°C) intermediate layer (CIL). In the southwestern GSL, the CIL is a large volume of water sandwiched between the coastal water and the deep water located in the Laurentian channel. The top of the layer ranges from 20 to 40 m depth from June to October and rises to the surface from January to April (Gilbert and Pettigrew, 1997). As it was hypothesized by Stasko (1980), there seems to be no advantage in long-distance movement to deeper water (>40 m) for lobsters in the GSL because it is cold (<1.5°C) in both summer and winter (CIL). Although lobsters can tolerate temperatures ranging from –1.5° to 30°C, at temperatures below 0°C they are in a state of hibernation, and below 5°C molt induction is blocked (Waddy et al., 1995). It is clear that lobsters can "tolerate" cold temperature but to be active they need warmer waters. Lobster movements of more than 40 km were rare in the southwestern GSL and movements exceeding 70 km through deep, colder waters (>40 m) were not observed. In contrast, lobsters from the Bay of Fundy, from coastal waters of southwestern Nova Scotia, and from coastal waters off New England can take advantage of warmer temperatures in deep waters in the Gulf of Maine and on the continental shelf during the winter (Campbell and Stasko, 1986). Campbell and Stasko (1985) and Campbell (1989) showed that lobsters tagged in the inshore waters of southwestern Nova Scotia traveled up to 240 km to the edge of the continental shelf off Georges Bank to depths below 200 m, seemingly without crossing a wide area of cold water. Similarly, lobsters tagged in the Bay of Fundy were also recaptured in deep waters at the edge of the continental shelf across the Gulf of Maine and along the coastal waters of the United States (Campbell and Stasko, 1986), at a distance of more than 780 km. These types of movements were not observed in the southwestern GSL. Lobster movements between mainland New Brunswick, Prince Edward Island, or Cape Breton, and the Magdalen Islands, for example, have not been reported. The Magdalen Islands are an archipelago with a substantial lobster fishery located in the middle of the southwestern GSL, surrounded by >60 m depths at about 80 to 90 km from Prince Edward Island, and Cape Breton. Lob-

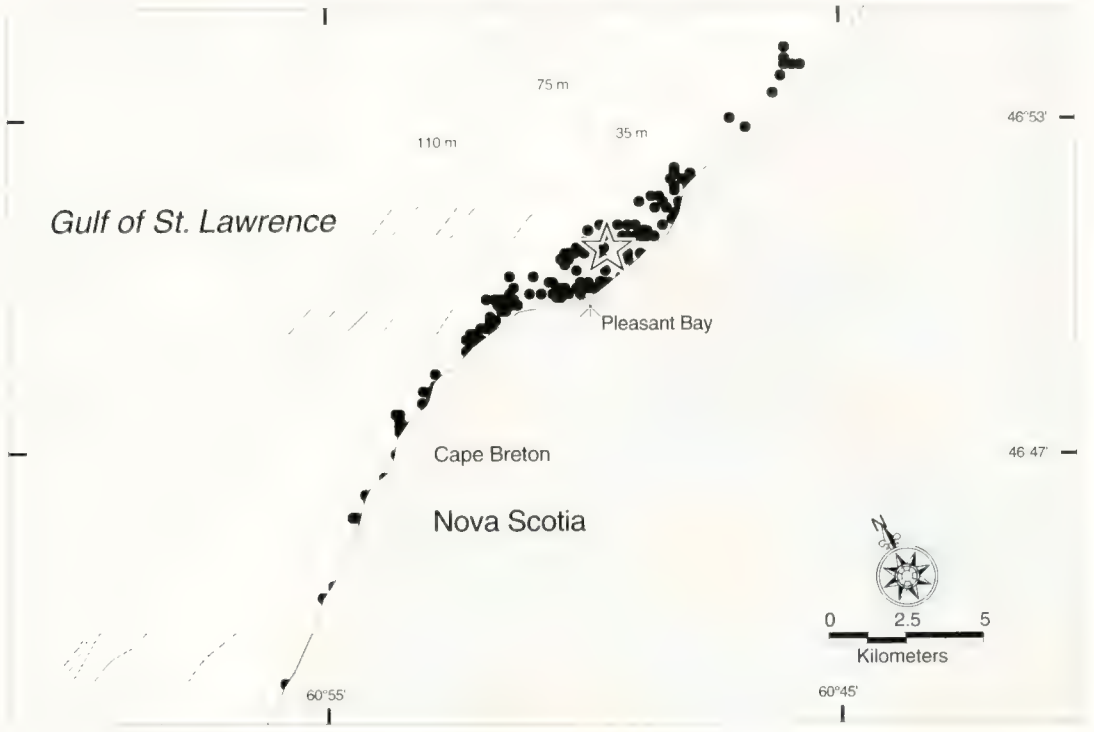

Figure 5

Locations (•) of tagged American lobsters recaptured in 1993 (n=777) from the 1992 tagging project conducted in Pleasant Bay, Nova Scotia. The release sites are indicated by a star symbol.

Figure 6

Location of tagged American lobsters recaptured in the Val Comeau and the Miramichi Bay area. Squares represent lobsters recaptured from the 1996 Val Comeau (n=127) tagging project, circles represent lobsters recaptured from the 1996 Neguac (n=74) tagging project, and triangles represent lobsters recaptured from the 1997 Escuminac (n=17) tagging project. The release sites are indicated by a star symbol.

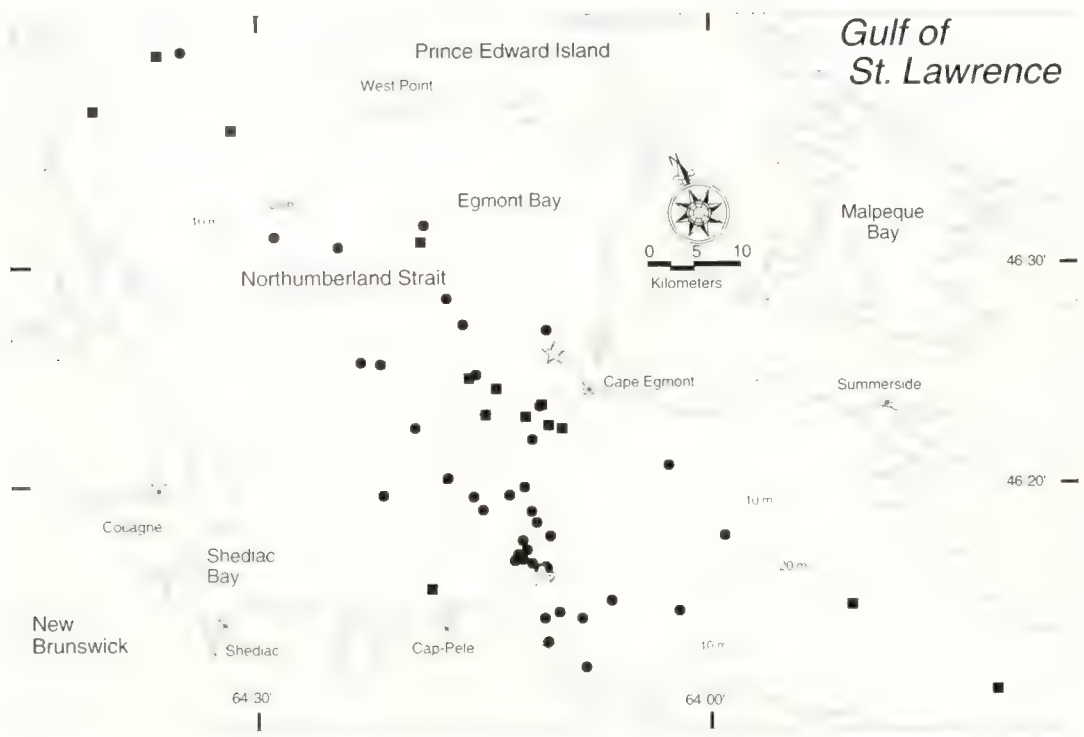

Figure 7

Location of tagged American lobsters recaptured in central Northumberland Strait. Squares represent lobsters recaptured from the Egmont Bay (n=15) tagging project and circles represent lobsters recaptured from the Cap-Pelé (n=41) tagging project, conducted in 1982 and 1997, respectively. The release sites are indicated by a star symbol.

ster movements in the southwestern GSL seem to be temperature-dependent because the cold waters of the CIL appeared to be an effective barrier to movements between the shallow waters of the Magdelan Islands and the shallow coastal waters of the rest of the southwestern GSL.

The distances traveled by lobsters (>60 mm CL) in the southwestern GSL were not sex- or size-dependent, except for berried females. Similar to our findings, the results of most recent studies do not indicate significant differences between the distance traveled in relation to size or sex for lobsters tagged in coastal waters (Fogarty et al., 1980; Krouse, 1981; Campbell, 1982; Tremblay et al., 1998). In contrast, Templeman (1935) and Bergeron (1967) suggested that lobster movements were sex-dependent, but neither author reported whether the differences were supported in a statistical or biological sense. Campbell and Stasko (1985, 1986) and Campbell (1989) indicated that lobster movements were size-dependent because they observed that large mature animals (≥95 mm CL) on average traveled significantly farther than small immature ones. They explained that mature animals would move more extensively to reach the warmest seasonal temperature to maximize their degree-days (the accumulative sum of daily mean temperatures recorded above 0°C) needed for somatic and gonadic development. This was not the case in our study. We observed, however, that on average berried females in the southwestern GSL traveled shorter distances than males and nonberried females. Saila and Flowers (1968) indicated that the distance traveled by berried females was related to their physiological state. In a tagging experiment, they captured berried females on the continental shelf, tagged, and released them in the inshore waters off the coast of Rhode Island at about 220 km from their captured position. When females were carrying eggs, they traveled only short distances within the inshore waters. Once they shed their eggs, however, these females returned to the continental shelf where they were originally captured. Berried females tagged in inshore waters in the Magdalen Islands (Munro and Therriault, 1983), Jeddore Harbour and Clam Bay, Nova Scotia (Jarvis, 1989), and New Hampshire (Watson et al., 1999) also traveled short distances. In the Cape Cod area, berried females tagged in the inshore waters were reported to have traveled an average distance of 30 km, mostly parallel to the coast (Morrissey, 1971; Estrella and Morrissey, 1997). Off Grand Manan Island, Campbell (1986, 1990) reported relatively small inshore–offshore migration, less than 15 km, for 75% of the berried females and attributed this migration to an effort to maximize egg development by exposure to warmer water. In general, it seems that the condition of carrying eggs could influence the extent of movements in the southwestern GSL, not the size or sex of the animal.

In terms of fishery management, there is relatively little interaction between lobsters at different LFAs at the benthic level because lobster traveled on average small

distances. The main concern of fishermen in the southwestern GSL was the minimal legal size (MLS) disparity between LFA 24 (MLS of 63.5 mm CL) located on the north side of Prince Edward Island and the other LFAs (MLSs from 65.1 to 70.0 mm CL). More precisely, they were interested in lobster movements in relation to time, i.e. if lobsters released in a given area in one season would be recaptured in the same area in future seasons. From our findings, lobsters do not move farther if they are at large for a longer period. Distances traveled by lobsters were not time-dependent for lobsters at large between 200 (with at least one winter season) and 1102 days. Results of our tagging studies were consistent with results from earlier studies carried out in the southwestern GSL and demonstrated that lobsters in their benthic stages have little long distance interaction. Hence, lobster movements in the southwestern GSL should have minimal consequences in terms of lobster management.

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Abstract–Shortspine thornyhead (*Sebastolobus alascanus*) abundance was estimated from 107 video transects at 27 stations recorded from a research submersible in 1991 off southeast Alaska at depths ranging from 165 to 355 m. Numbers of invertebrates in seven major taxa were estimated, as was substrate type. Thornyhead abundance ranged from 0 to 7.5/100 m^2, with a mean of 1.22/100 m^2, and was positively correlated with depth and amount of hard substrate. Invertebrate abundances were not significantly correlated with numbers of thornyheads. Shortspine thornyhead abundance estimates from this study were several times higher than estimates produced by bottom trawl surveys off southeast Alaska in 1990 and 1993, the two years of survey that encompassed the submersible transects; however, the trend of increasing abundance with depth was similar in the trawl surveys and in the submersible transects, suggesting that trawl surveys systematically underestimate abundance of shortspine thornyheads.

Shortspine thornyhead (*Sebastolobus alascanus*) abundance and habitat associations in the Gulf of Alaska

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Fish distributions are affected by physical conditions such as depth, temperature and substrate type and by biotic variables such as prey distribution, predator presence, and habitat features (e.g. kelp forests). Patterns of habitat use are important factors in resource assessments, and stratification based on habitat characteristics are common features of survey design. For example, trawl surveys in the Gulf of Alaska are stratified by depth and general bottom type (flats, gullies, shelf break, slope) (Stark and Clausen, 1995). Assessment of fish populations based on traditional fishing gear, such as trawls or longlines, provide relatively economical surveys with broad geographic coverage; however, they provide limited detailed information on species associations or habitat preferences (Matlock et al., 1991).

Shortspine thornyhead (*Sebastolobus alascanus*) is a member of the family Scorpaenidae, which includes the rockfishes (*Sebastes*—over 60 species in the northeast Pacific) and three species of thornyheads (*Sebastolobus*). Shortspine thornyhead range from Baja California, Mexico, to the Bering Sea and are found at depths to 1500 m (Moser, 1974). Off southeast Alaska, most fish sampled from 200–310 m depths were between 15 and 30 years old and had lengths of 25–35 cm (Miller, 1985). The maximum age observed by Miller (1985) was 62 years, and age at 50% maturity was 12 years for both sexes. These life-history features are similar to those of rockfishes, and such long-lived fishes are difficult to manage because they are easily overexploited and recover slowly from overfishing (Adams, 1980). Shortspine thornyhead have been commercially valuable in the Gulf of Alaska, where catch (including discards) ranged from 1298 to 2020 metric tons from 1991 to1996 (Ianelli and Ito[1]). Bycatch of thornyhead has the potential of forcing closure of other high-value fisheries (Ianelli and Ito[2]). Estimates of their abundance and size distribution are currently based on bottom trawl and longline surveys (Ianelli and Ito[2]); however, direct observations from submersibles can provide an alternate method for assessing abundance (Krieger, 1993). Assessments of thornyheads and rockfishes often result in population estimates with high variances; resulting in considerable uncertainty for assigning

[1] Ianelli, J. N., and D. H. Ito. 1998. Status of Gulf of Alaska thornyheads (*Sebastolobus* sp.) in 1998. *In* Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska, p. 371–402. [Available from North Pacific Fishery Management Council, 605 West 4th St., Anchorage, Alaska 99501.]

[2] Ianelli, J. N., and D. H. Ito. 1994. Thornyheads. *In* Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska for 1995. [Available from North Pacific Fishery Management Council, 605 4th St., Anchorage, Alaska 99501.]

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Figure 1

Locations of stations (•) where transects were run off southeast Alaska. The offshore line marks the 200-m isobath near the edge of the continental shelf.

harvest levels. Submersible observations with line-transect methods have been used in attempts to improve estimates of rockfish abundance and to understand rockfish habitat associations (Richards, 1986; Pearcy et al., 1989; Krieger, 1992; Stein et al., 1992; O'Connell and Carlile, 1993).

Our goal was to assess abundance and habitat use by shortspine thornyhead in the eastern Gulf of Alaska, based on data from existing video records taken during submersible transects. We estimated abundance of fish and invertebrates and quantified substrate type. We explored the relationships between thornyhead abundance and both physical and biotic environmental variables and compared abundance estimates from submersible transects with those from trawl surveys in the same area.

Materials and methods

Sources of data were video tapes of 107 bottom transects recorded at 27 stations during submarine dives in June 1991 on the outside coast of northern southeast Alaska from Cape Ommaney to Yakatat (Fig.1). All transects were conducted with the Delta submersible. This battery-powered two-man submersible is 4.7 m long, dives to 365 m, and travels 2–6 km/h. It is equipped with ten 150 W external halogen lights, internal and external video cameras, a 35-mm external camera, magnetic compass, directional gyro compass, and underwater telephone and transponder that allowed the submersible to be tracked from the surface support vessel. The surface vessel recorded LORAN fixes at the beginning and end of each transect. A pilot and observer formed the crew of the submersible: the pilot attempted to maintain the submersible within 0.5 m above the bottom at 3–4 km/h while the observer made observations through a starboard porthole.

Video recordings were made from a downward projecting external Hi-8 color video camera tilted obliquely forward on the starboard side and included a digital readout of depth, temperature, and height above bottom. Data were collected either in strip transects by using the entire length of each transect, or in quadrats by freezing individual frames from the video. The width of the strip transect was calculated from the height above bottom and field of view of the camera. The field of view formed a trapezoid on the seafloor beginning almost directly beneath the camera and projecting forward; its maximum width (W) was estimated by calibrations performed on a subsequent cruise that had the same camera and camera configuration (Zhou and Shirley, 1997). When the submarine was resting on the bottom, the camera height (H) was 0.93 m and the width of the field of view (i.e. longest side of trapezoidal field) was 1.78 m. Transect width (W) was estimated by

$$W = (1.78/0.93)\,H, \qquad \text{[(Zhou and Shirley, 1997)]}.$$

The height above bottom (H) was recorded at one minute intervals during each transect and mean height was used to estimate width (W) of that transect. All dives were made during daylight between 0600 and 1900 h. At each station a series (usually 4) of parallel transects was run, and spacing between transects was about 200 m. Transect lengths

were calculated from the position fixes taken from the surface vessel.

The entire length of each transect was viewed and all thornyheads in the field of view were counted. Invertebrates were also counted in seven categories: starfish, seapens, sea urchins, anemones, corals, sponges, and sea cucumbers. Depth and temperature were recorded once every minute during each transect and averaged over the complete transect. Substrate type was estimated by scoring video quadrats at one-minute intervals during the transect. A mylar grid of about twenty-five 50-mm squares was placed on the screen over the freeze-framed image, and substrate within the squares was scored in three categories of soft (mud, sand, and gravel), cobble, and rock-boulder, the latter two of which were then combined into a single category, hard-bottom. The proportions of each category (soft and hard) for each transect were estimated as the mean from the one-minute quadrats. Abundance (number/100 m^2) of shortspine thornyheads and invertebrate categories was estimated for each transect by dividing the number counted by the area estimate ($W \times Transect\ length \times 100$).

To evaluate variables that may have affected thornyhead densities, we assembled a correlation matrix and a partial correlation matrix of three physical variables (depth, substrate, temperature) and transformed ($\log(x+1)$) biotic variables (shortspine thornyheads and seven invertebrate categories). Based on those matrices, we selected depth and substrate for further analyses.

We used nonparametric procedures (Kruskal-Wallis and Mann-Whitney) to determine if thornyhead densities varied among sampling stations and to evaluate the effects of substrate and depth. Substrate and depth were coded into nominal categories for use as independent variables in those analyses. We used Scheffe's (Zar, 1984) *post-hoc* test to evaluate between-category differences when Kruskal-Wallis results were significant.

An ANOVA factorial model was used to explore the joint effects depth and substrate on shortspine thornyhead abundance (transformed by $\log(x+1)$). In addition, we used stepwise linear regression with thornyhead abundance as the dependent variable to evaluate the relative importance of all possible independent variables.

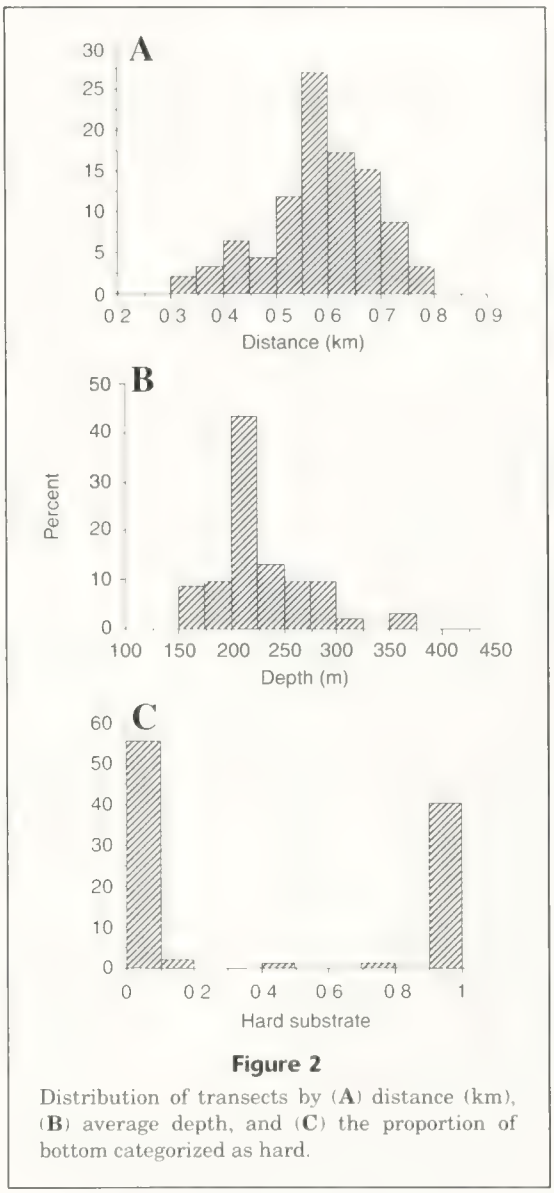

Figure 2

Distribution of transects by (**A**) distance (km), (**B**) average depth, and (**C**) the proportion of bottom categorized as hard.

Results

Transect lengths ranged from 320 to 800 m and had a mean of 580 m (Fig. 2A). The mean transect depth ranged from 165 to 355 meters, and the highest numbers of transects were at 200–250 m (Fig. 2B). Most transects (85%) had substrate that was completely soft (silt, sand, and gravel) or hard (cobble and rock-boulder) (Fig. 2C). Abundance of shortspine thornyheads per transect ranged from 0 to 13.6/100 m^2; and the mean abundance at the 27 stations ranged from 0 to 7.5/100 m^2 (Table 1). Difference in abundance among stations was very highly significant (P <0.0001, Kruskal-Wallis).

A correlation matrix of all variables indicated that depth, substrate, and sponge abundance were related to variation in thornyhead abundance; however, the partial correlation matrix indicated that among those three variables, substrate type and depth were most strongly related to shortspine thornyhead abundance (Table 2). The high correlation of sponge and thornyhead abundances was apparently spurious because of the relationship between sponge abundance and substrate type (Table 2).

For further analyses of the relationship between thornyhead abundance, depth, and substrate, we coded depth into three nominal categories, <200 m, 200–300 m, and >300m, chosen to correspond to the depth intervals used in National Marine Fisheries Service (NMFS) triennial trawl surveys (Stark and Clausen, 1995). We also coded substrate into two nominal categories, soft bottom (>90% sand, mud, and gravel) and hard bottom (>40% cobble and rock-boulder). Abundance increased with depth (Table 3), and differences that were highly significant occurred among three depth categories (P<0.001, Kruskal-Wallis). Significant differences exist-

Table 1

Mean numbers, with standard deviation, of shortspine thornyheads (*Sebastolobus alascanus*) per 100 m^2 at transect stations, with means of depth, bottom temperature, and proportion of the bottom categorized as hard substrate.

Station	n	No./100 m^2	SD	Mean depth (m)	Temp.	Proportion of bottom as hard substrate	Lat.	Long.
55	4	0.4	0.002	210.1	4.00	0.27	56°37′11″	135°57′50″
56	4	0.5	0.002	209.0	4.33	0.00	56°32′19″	135°54′39″
57	4	2.7	0.007	319.9	3.83	1.00	56°06′06″	135°39′72″
59	4	0.2	0.002	280.1	4.51	0.00	55°46′03″	134°77′97″
60	4	0.0	0	227.9	4.83	0.00	55°61′28″	134°55′86″
61	4	0.0	0	202.9	4.90	0.00	55°71′53″	134°76′89″
62	4	0.0	0	165.5	5.42	1.00	55°86′00″	134°84′00″
63	4	0.9	0.004	355.9	4.04	0.04	55°98′36″	134°93′97″
64	4	3.8	0.011	220.3	4.86	0.78	56°80′97″	135°80′97″
65	4	2.5	0.007	237.9	4.73	0.54	56°69′22″	135°87′69″
67	3	2.6	0.012	247.9	3.95	0.11	57°24′72″	136°29′31″
68	4	3.6	0.02	246.2	4.50	0.75	57°21′67″	136°25′03″
69	4	7.5	0.045	242.7	4.53	0.72	57°55′33″	136°55′22″
70	4	0.7	0.01	217.7	4.84	0.20	57°95′94″	137°21′61″
71	4	0.1	0.002	177.4	4.95	1.00	58°02′00″	137°10′00″
72	4	0.1	0.001	289.9	4.02	0.00	58°10′92″	136°98′39″
73	4	1.2	0.007	210.8	4.79	1.00	59°03′75″	141°13′75″
75	4	0.1	0.001	208.4	4.25	0.86	59°24′50″	141°62′14″
77	4	2.9	0.015	299.8	3.76	0.71	59°31′44″	142°11′42″
78	4	0.0	0	205.8	4.25	0.77	59°22′22″	141°70′86″
79	4	0.0	0	183.9	4.67	0.51	58°00′00″	140°50′00″
80	4	0.4	0.001	251.4	4.43	0.00	58°66′81″	139°37′33″
81	4	0.3	0.002	208.4	5.04	0.00	58°65′61″	139°56′08″
82	4	0.3	0.001	262.8	4.59	0.00	58°53′81″	139°61′56″
83	4	0.0	0	218.9	4.81	0.00	58°35′00″	139°32′89″
84	4	0.0	0	172.4	5.32	0.76	58°22′00″	139°00′00″
85	4	2.4	0.016	215.2	5.26	0.74	58°10′17″	138°65′33″

ed between the shallowest depth category and both deeper depth groups (Table 3, Sheffe test). Substrate type also affected abundance (Table 3); transects with hard substrate had a significantly higher density of thornyheads than transects on soft bottom (P=0.016, Mann-Whitney). There was a significant interaction (P=0.01) of depth and substrate in the ANOVA factorial analysis (Table 4) due to the sharp increase in thornyhead abundance in depths >200 m on the hard substrate than on the soft substrate (Fig. 3).

Stepwise multiple regression with all variables resulted in a model that incorporated two variables: substrate type and depth, with substrate type entered first. The final two-variable regression model was

$$A = 0.017\,S + 0.00016\,D - 0.033, \qquad [r^2=0.208]$$

where A = thornyhead abundance;
S = proportion of bottom that is hard substrate; and
D = depth (m).

Thornyhead abundance increased with depth and amount of hard substrate, although there was an indication that abundance may have reached maximum levels at depths of 200–300 m (Fig. 3).

Discussion

Film (still or motion) and videotape recordings of transects have been used to assess abundance of aquatic organisms (Auster et al., 1989; Butler et al.[3]). Potential biases in such data include systematic underestimation

[3] Butler, J. L., W. W. Wakefield, P. B. Adams, B. H. Robison, and C. H. Baxter. 1991. Application of line transect methods to surveying demersal communities with ROVs and manned submersibles. Proceedings of the IEEE Oceans '91 Conference, p. 689–696. Institute of Electrical and Electronic Engineers, Piscataway, NJ.

Table 2

Correlation (lower left diagonal) and partial correlation matrices (upper right diagonal) for shortspine thornyhead (SSTH), depth, substrate type, temperature, and invertebrates. Significant correlations are indicated in bold.

	SSTH	Depth	Substrate	Temperature	Sea star	Urchin	Sea pen	Anemone	Coral	Sponge	Cucumber
SSTH		0.35	0.37	0.08	−0.13	0.24	0.04	−0.13	0.04	0.27	−0.12
Depth	**0.23**		−0.34	−0.56	0.02	0.03	0.00	0.09	−0.16	−0.08	0.11
Substrate	**0.32**	**−0.31**		0.00	−0.12	−0.16	−0.01	0.39	−0.15	0.23	0.25
Temp.	−0.10	**−0.62**	0.17		−0.02	−0.07	0.24	0.04	−0.05	−0.15	−0.22
Seastar	−0.18	0.05	−0.16	−0.04		0.23	0.18	0.24	0.04	−0.06	0.01
Urchin	0.11	0.18	**−0.21**	−0.12	**0.35**		0.19	0.04	0.08	−0.13	−0.04
Sea pen	−0.01	−0.09	0.04	0.13	**0.36**	**0.33**		−0.06	0.35	0.10	0.43
Anemone	0.00	−0.07	**0.38**	0.03	**0.22**	0.04	0.15		0.07	0.07	0.09
Coral	−0.05	−0.09	−0.03	0.03	**0.30**	**0.27**	**0.61**	0.16		0.05	0.27
Sponge	**0.37**	−0.08	**0.41**	−0.02	−0.18	−0.16	−0.02	0.14	−0.04		−0.17
Cucumber	−0.06	0.08	0.13	−0.15	0.27	0.20	**0.59**	**0.24**	**0.53**	−0.09	

Table 3

Mean abundance (number/100 m^2) of shortspine thornyheads in three depth categories (Kruskal-Wallis, $P<0.0001$), and in two substrate categories (Mann-Whitney, $P=0.016$), with sample sizes and standard errors. Results of nonparametric analyses are included.

	Abundance	*n*	SE
Depth			
100–200	0.1	18	0.1
200–300	1.4	80	0.2
>300	1.9	9	0.4
Substrate			
soft	0.6	57	0.1
hard	1.9	50	0.4

Table 4

Factorial analysis of effect of depth and substrate (proportion of bottom categorized as hard substrate) on shortspine thornyhead abundance (number/100 m^2, $\log(x+1)$ transformed).

Variable	df	Sum of squares	*F*-value	*P*
Depth	2	1.01	10.28	<0.0001
Substrate	1	0.35	7.10	0.009
Depth-substrate interaction	2	0.41	4.17	0.018
Residual	101	4.96		

due to gear avoidance or overestimation due to attraction of fish to the submersible. The behavior of shortspine thornyheads observed in the videotapes from our study indicated that they were not affected by the submersible. They typically remained relatively motionless unless the submersible came very close (almost touching the fish). It is also unlikely that they had moved away, or toward, the submersible, before coming into the camera field. On all dives there was an observer and another video camera recording a broader area, and there was no indication that shortspine thornyheads were responding to the submarine. The passive behavior of shortspine thornyheads in response to submersibles has been noted previously (Krieger, 1992).

In transect assessments, the probability of detecting organisms typically is not equal over the entire field of view. Detection is affected by such factors as lighting, orientation of the organism and its reflectivity, sea floor relief, suspended particles, and size of the organism. Butler et al.[3] examined the detection functions for three types of fish (flatfish, hagfish, and thornyhead) from data collected off California. For thornyheads, the probability of detection was relatively constant to a distance of about 180 cm. This distance is larger than the width of the transects in our study, indicating that our use of a constant detection function (probability of 1.0) was appropriate.

We found that shortspine thornyheads preferred habitat with hard substrate. Submersible transects have been used to identify habitat used by rockfishes and thornyheads in the northeast Pacific Ocean (Richards, 1986; Pearcy et al., 1989; Stein et al., 1992; O'Connell and Carlile, 1993; Krieger and Ito, 1999). Off Oregon, thornyheads were included in an assemblage of fishes associated with mud bottom (Stein et al., 1992), and Pearcy et al. (1989) observed that in deep water they occurred on mud bottom, but in shallower water were found over both rock and mud. We have no explanation for the differences in habitat association between Oregon and southeast Alaska.

Our observations are based on a larger number of transects than those surveyed off Oregon, but the consistency of results from the two Oregon studies suggests that the difference is not due to a low sample size there. Our observation that abundance of shortspine thornyheads increases with depth is consistent with results from trawl surveys off Alaska, Oregon, and California (Martin and Clausen, 1995, Stark and Clausen, 1995, Jacobson and Vetter, 1996). Off Oregon, their abundance was highest in the 200–400 m depth zone, and decreased sharply between 400 m and 1400 m (Jacobson and Vetter, 1996). Off California, the highest abundance of shortspine thornyheads occurred at 400–600 m, probably because of the warmer waters off California (Jacobson and Vetter, 1996). Thus, our sampling depths covered the most important depth zones for this species in the waters off southeast Alaska, which are colder than those off Oregon.

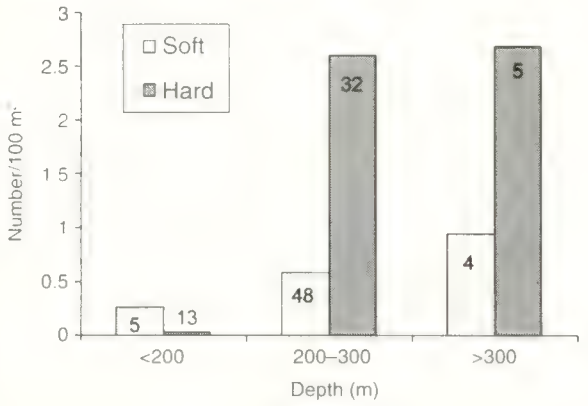

Figure 3

Mean abundance of shortspine thornyhead on soft and hard bottom substrates in three depth intervals. Sample size (number of transects) and standard errors are indicated in the number and vertical line over each bar.

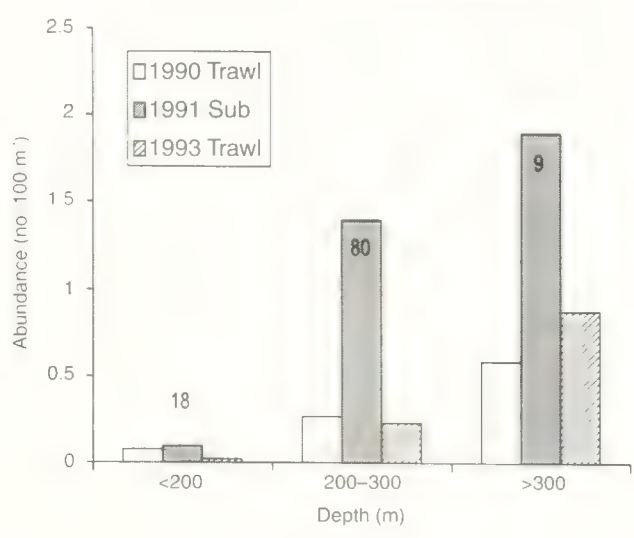

Figure 4

Mean abundance of shortspine thornyhead in three depth intervals from submersible transects in 1991 and from the 1990 and 1993 trawl surveys off southeast Alaska. Sample size (number of transects) and standard errors of the submersible estimates are indicated in the number and vertical line with each bar.

Bottom trawl surveys of fishes in the Gulf of Alaska are conducted triennially, and occurred one year before (1990) and two years after (1993) our submersible survey (Martin and Clausen, 1995; Stark and Clausen, 1995). For many species, trawl survey results may be biased because some species may be herded by the trawl doors into the path of the net, resulting in overestimates of abundance when the "area-swept" method is applied (Krieger, 1992). Other fish in the water column above the bottom may swim over the net and be underestimated by the survey (Balsiger et al., 1985). Escape routes under the foot rope and through the larger meshes in the trawl wings are also possibilities.

The NMFS trawl survey does not cover exceptionally rugged rocky habitats that would destroy equipment; consequently, species that select high-relief habitats may be underestimated by the survey, whereas species that select low-relief soft-bottom habitats may be overestimated. Submersible observations provide a means to quantify the biases inherent in bottom trawl surveys. The depth categories we used to analyze the submersible data matched the depth strata used in the NMFS triennial trawl surveys. Mean abundance of shortspine thornyheads in submersible surveys were several times higher that those in the 1990 and 1993 trawl surveys; however, the ratios of abundance in the three depth zones were very similar (Fig. 4). We suggest that trawl surveys underestimate the abundance of shortspine thornyheads in the Gulf of Alaska but may be good indicators of relative abundance, patterns of distribution, and stock trends.

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Abstract—Analysis of 32 years of standardized survey catches (1967–98) indicated differential distribution patterns for the longfin inshore squid (*Loligo pealeii*) over the northwest Atlantic U.S. continental shelf, by geographic region, depth, season, and time of day. Catches were greatest in the Mid-Atlantic Bight, where there were significantly greater catches in deep water during winter and spring, and in shallow water during autumn. Body size generally increased with depth in all seasons. Large catches of juveniles in shallow waters off southern New England during autumn resulted from inshore spawning observed during late spring and summer; large proportions of juveniles in the Mid-Atlantic Bight during spring suggest that substantial winter spawning also occurs. Few mature squid were caught in survey samples in any season; the majority of these mature squid were captured south of Cape Hatteras during spring. Spawning occurs inshore from late spring to summer and the data suggest that winter spawning occurs primarily south of Cape Hatteras.

Geographic and temporal patterns in size and maturity of the longfin inshore squid (*Loligo pealeii*) off the northeastern United States

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The longfin inshore squid, *Loligo pealeii*, is distributed in the northwest Atlantic from Canada to the Caribbean (Cohen, 1976). Within its range of commercial exploitation (from southern Georges Bank to Cape Hatteras) the population is considered to be a unit stock (NEFC[1]), although heterogeneous subpopulations may exist (Garthwaite et al., 1989).

North of Cape Hatteras, *L. pealeii* migrate seasonally. The migration has been described as a movement offshore during late autumn (so that the species can overwinter in warmer waters along the edge of the continental shelf) and a return movement inshore during the spring and early summer (Summers, 1969; Serchuk and Rathjen, 1974; Tibbetts, 1977). Murawski (1993) defined *L. pealeii* as a member of a migratory, warm-water group of species, centered primarily in mid-Atlantic waters (particularly in the spring), that make inshore and northward migrations in the spring and offshore and southward migrations in late autumn.

Geographic patterns in Northeast Fisheries Science Center (NEFSC) survey catches, from the Gulf of Maine to Cape Hatteras, show that *L. pealeii* are distributed over the entire continental shelf (from inshore to offshore) in the autumn, are concentrated at the edge of the continental shelf and at the southern end of the survey area during winter and spring, and are concentrated inshore in summer (Summers, 1967; 1969; Serchuk and Rathjen, 1974; Vovk, 1978; Lange, 1980; Whitaker, 1980; Lange and Waring, 1992).

Analyses of survey catches indicate that depth, time of day, and temperature all influence cross-shelf distribution patterns (Summers, 1969; Serchuk and Rathjen, 1974; Lange and Waring, 1992; Murawski, 1993; Brodziak and Hendrickson, 1999). Diel correction factors have been applied to survey indices in various studies to adjust nighttime bottom trawl catches to daytime equivalents (daytime catches are higher when squid are concentrated close to the bottom) (Lange and Sissenwine1983; Lange and Sissenwine[2]). Research by Lange and Waring (1992) and Brodziak and Hendrickson (1999) demonstrated that the diel differences were size specific and that further consideration of these differences in correction factors was warranted.

Until recently, *L. pealeii* was thought to have a life span of up to three years, and the stock was assessed accordingly (Sissenwine and Tibbetts, 1977; Lange, 1981; Lange and Sissenwine,

[1] NEFC (Northeast Fisheries Center). 1986. Report of the second NEFC stock assessment workshop. NEFC Lab. Ref. Doc. 88-02, 114 p. [Available from NEFSC, 166 Water Street, Woods Hole, MA 02543.]

[2] Lange, A. M. T., and M. P. Sissenwine. 1977. *Loligo pealei* stock status. Northeast Fisheries Science Center Lab. Ref. Doc. 77-28, 9 p. [Available from NEFSC, 166 Water Street, Woods Hole, MA 002543.]

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Fish. Bull. 200–213 (2002).

1983; Lange[3]; Lange et al.[4]). Recent advances in the use of statoliths for age determination of squid (see reviews in Rodhouse and Hatfield, 1990; Jereb et al., 1991; Jackson, 1994) have enabled new estimates of life span to be derived for *L. pealeii* (Macy, 1995; Brodziak and Macy, 1996; Macy[5]), which indicate that the life span of *L. pealeii* can be less than nine months. Back-calculations of hatching date from age data revealed that there is more than just a spring-summer spawning component of the population (Brodziak and Macy, 1996; Macy[5]), with a small proportion of squid hatching during winter. This winter spawning is presumed to occur offshore (Brodziak and Macy, 1996), in the vicinity of the submarine canyons along the edge of the northeastern U.S. continental shelf, from Hudson Canyon up to Georges Bank (Fig. 1). The possibility of winter spawning was raised initially by Summers (1969), based on length-frequency data, but squid were not presumed to spawn until their second year because their growth was assumed to be too slow to allow spawning during their first summer.

Our study reports on two studies: 1) an analysis of survey data from spring and autumn NEFSC surveys from 1967 to 1998, and from winter NEFSC surveys from 1992 to 1998, to describe gross distribution patterns of *L. pealeii* over the northwest Atlantic continental shelf from Cape Hatteras to the Gulf of Maine; 2) some results of a field study initiated in 1997 to investigate geographic and seasonal patterns of growth and maturity to determine if the winter spawning component off the northeastern United States can be defined by time and area.

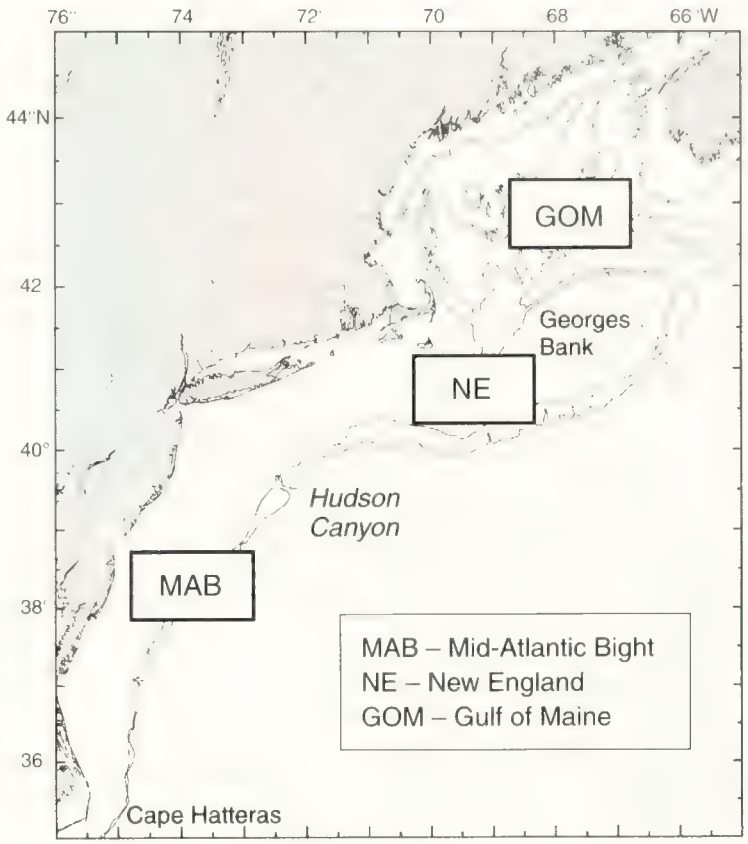

Figure 1

Map of the survey areas for longfin inshore squid off the northeastern coast of the United States (1967–98).

Materials and methods

Survey analysis

Length-frequency data for *L. pealeii* were analyzed from NEFSC bottom-trawl surveys conducted in the autumn (generally from mid-September to late October) from 1967 to 1997; in the spring (generally from March to early April) from 1968 to 1998; and in the winter (generally in February) from 1992 to 1998. Data collection and processing and archiving methods are described by Azarovitz (1981). In the autumn and spring surveys the same trawl-sampling gear (Yankee-36 trawl) has been used since 1967, except during 1973–81, when a Yankee-41 (high rising) trawl was substituted in the spring surveys. In the winter surveys the trawl gear was larger and the Gulf of Maine was not sampled.

The NEFSC survey area was divided into two geographic regions (the region north of Hudson Canyon to the Gulf of Maine [designated New England, NE] and the region south of Hudson Canyon to Cape Hatteras (designated Mid-Atlantic Bight [MAB]) and into four bottom depth zones (27–55 m, 56–110 m, 111–185 m, and 186–366 m [Fig. 1]). The 1–26 m depth zone was not sampled in NEFSC offshore surveys, but "inshore" strata were added to the survey in 1972.

For the spring and winter surveys, the combined effects of annual abundance (numbers of squid per standardized trawl haul), survey stratum, and time of day (night, 20:00–03:59; dawn and dusk, 04:00–07:59, 16:00–19:59; and day, 08:00–15:59), as described by Brodziak and Hendrickson (1999) for the autumn survey, were analyzed to determine adjustment factors for diel differences in log-transformed survey catches of prerecruit squid (≤80 mm dorsal mantle length [ML], the minimum size in commercial catches) and recruits (>80 mm ML). The derived factors were then used to adjust all survey catches to

[3] Lange, A. M. T. 1984. An assessment of the long-finned squid resource off the northeastern United States. Northeast Fisheries Science Center (NEFSC) Lab. Ref. Doc. 84-37, 24 p. [Available from NEFSC, 166 Water St. Woods Hole, MA 02543.]

[4] Lange, A. M. T., M. P. Sissenwine, and E. D. Anderson. 1984. Yield analysis of long-finned squid, *Loligo pealei* (LeSueur). Northwest Atlantic Fisheries Organization (NAFO) SCR Doc. 84/IX/97, 29 p.

[5] Macy W. K. 1995. Recruitment of long-finned squid in New England (USA) waters. ICES CM 1995/K:35, 18 p. [Available from W. K. Macy, Graduate School of Oceanography, Univ. Rhode Island, South Ferry Road, Narragansett, RI 02882].

their daytime equivalent. The size groups (≤80 mm ML, >80 mm ML) were chosen to allow comparisons with results from previous studies (e.g. Lange, 1980; 1981; Lange and Sissenwine, 1983; Brodziak and Hendrickson, 1999; NEFC[1]; Lange and Sissenwine[2]; Lange[3]). Alternative analyses were performed for different size groups (≤50 mm ML, >50 mm ML and ≤100 mm ML, >100 mm ML) to assess the sensitivity of the results to the choice of size groups. The combined effects of geographic region (NE and MAB), depth zone, and year on survey catches were tested by using generalized linear models (GLM) to derive main effects and coefficients for each survey. Pairwise comparisons were tested by using a *t*-test with Bonferroni adjustments (Sokal and Rohlf, 1995) to compare specific regions, seasons, and depth zones. All tests were analyzed at the 5% significance level. Differences between seasons and regions were tested between autumn and spring surveys for the years 1968 to 1997, between autumn and winter for 1992 to 1997, and between spring and winter surveys from 1992 to 1998. Proportion of catches ≤50 mm ML were analyzed to evaluate the relative distribution of juvenile *L. pealeii*.

Biological analysis

Subsamples of 50–100 individuals were obtained from five different survey time series: NEFSC autumn (September–October 1997), winter (February 1998), and spring (March 1998), inshore Massachusetts (Howe[6]) (October 1997), and Connecticut (Johnson[7]) (Long Island Sound, May 1998). The samples were analyzed from each of five depth zones (1–26 m, 27–55 m, 56–100 m, 111–185 m, 186–366 m), within each of three geographic regions (Gulf of Maine [GOM]; Georges Bank–Southern New England, north of Hudson Canyon [SNE]; and Mid-Atlantic Bight, see above [MAB]). A fourth region, south of Cape Hatteras (SOH) was added later. Each sample comprised a nonrandom selection of lengths to represent the size range present in a tow. In total, 2156 individuals were subsampled from 53 survey tows. Sexes were determined and specimens were measured to enable the morphometric maturity analyses of Macy (1982); each individual squid was also weighed on a top-loading balance to 0.1 g. The morphometric method uses a suite of length measurements for female and male squid to determine maturity stage (measured on a scale of 1 to 4, where 1 is immature and 4 is fully mature). Opportunistic commercial samples from early winter (December 1998 and January 1999) were also analyzed (118 individuals) to bridge the temporal gap in survey coverage.

Data on dorsal mantle length (ML, mm) and total body mass (BM, g) for each maturity stage were used to estimate proportions for each maturity stage across the length and weight range. These proportions were used to determine the sizes at which squid of both sexes changed from one maturity stage to the next.

Maturity-at-length data were weighted by diurnally adjusted catch-at-length data for each depth zone and region to provide population-weighted maturity patterns, assuming that survey length distributions accurately represent relative proportions of population components. Catch-weighted data were analyzed to derive 1) the patterns of maturity for each sex at different times of the year; 2) estimates of proportions of each maturity stage sampled by survey; 3) mean length for each maturity stage of each survey; 4) mean length for each region of each survey; and 5) mean length for each depth stratum of each survey. A small proportion (8.4%) of survey catches ≤50 mm ML were not subsampled; these were assigned to the juvenile stage. Catches at larger sizes, which were not subsampled (6.8% of survey catches), were removed from the analysis because sex or maturity stage could not be assigned with any degree of certainty. Individual squid, or size classes of squid, were not weighed during NEFSC surveys; therefore the maturity data from the biological analysis could only be catch-weighted by length because length was measured on a random subsample of squid caught at each station in NEFSC surveys.

Results

Survey analysis

Patterns of diurnal distribution were different among seasons surveyed (Table 1). In winter surveys, from 1992 to 1998, prerecruit (i.e. ≤80 mm ML) catch was lower at night and during dawn and dusk than during daylight hours (65% and 81% of daytime catch, respectively). However, for recruits (i.e. >80 mm ML), catch was higher both at night and at dawn and dusk than during the day (131% and 115% of daytime catch respectively) in winter surveys. In autumn and spring surveys, from 1968 to 1998, both prerecruits and recruits showed a lower catch at night and during dawn and dusk than by day; recruits showed a lesser diurnal variation than prerecruits. Results from analyses with different size groups (≤50 mm ML, >50 mm ML and ≤100 mm ML, >100 mm ML) were very similar, suggesting that the interaction of size and time of day is gradual.

Catch rates varied significantly by season (Table 2). During winter and spring, survey catches were greater in the MAB by a factor of approximately four (Fig. 2). However, there was no significant difference in survey catches between geographic regions in autumn (Fig. 2). Pairwise comparisons showed that mean number-per-tow was significantly greater in autumn than in spring within both geographic regions and was greater in autumn than in winter in the NE. There were no significant differences between autumn and winter means in the MAB nor between spring and winter means in either the MAB or the NE.

Catch by depth, pooled over the MAB and NE, varied by season (Table 3). Pairwise comparisons of each depth for each season showed that winter and spring survey catches were lowest in the shallowest stratum (27–55 m), in-

[6] Howe, A. B. 1989. State of Massachusetts inshore bottom trawl survey. Atlantic States Marine Fisheries Commission (ASMFC) Spec. Rep. 17:33–38. [Available from ASMFC, 1444 Eye Street, N.W., sixth floor, Washington, DC 20005.]

[7] Johnson, M. 1994. State of Connecticut marine finfish trawl survey. Atlantic States Marine Fisheries Commission (ASMFC) Spec Rep. 35:24–26. [Available from ASMFC, 1444 Eye Street, N.W., sixth floor, Washington, DC 20005.]

Table 1

Relative catch rates for small (≤80 mm dorsal mantle length (ML)) and large (>80 mm ML) *Loligo pealeii* in three seasonal NEFSC bottom-trawl surveys, 1967–98, by time of day (in relation to catch rates during daytime).

	Winter		Spring		Autumn	
Time of day	≤80 mm	>80 mm	≤80 mm	>80 mm	≤80 mm	>80 mm
Night	0.65	1.30	0.51	0.72	0.09	0.34
Dawn and dusk	0.81	1.14	0.79	0.92	0.46	0.83
Day	1.00	1.00	1.00	1.00	1.00	1.00

Table 2

Results of generalized linear model (GLM) of survey mean numbers-per-tow by year, depth zone, and geographic region (df=degrees of freedom; SS=sum of squares; *F*=*F*-statistic; *P*=probability), for *Loligo pealeii* off the northeast United States, based on NEFSC bottom-trawl survey data, 1967–98.

Season and effect	df	Type III SS	Mean square	*F*	*P*
Winter					
year	6	42.51	7.09	2.71	0.0133
depth	3	339.62	113.21	43.36	0.0001
region	1	233.73	233.73	89.53	0.0001
Spring					
year	30	409.47	13.64	4.44	0.0001
depth	3	1696.53	565.51	183.79	0.0001
region	1	983.51	983.51	319.64	0.0001
Autumn					
year	30	557.85	18.59	5.17	0.0001
depth	3	1134.09	378.03	105.20	0.0001
region	1	9.12	9.12	2.54	0.1113

Table 3

Diurnally adjusted, mean numbers-per-tow of *Loligo pealeii* from the three annual NEFSC bottom-trawl surveys, 1967–98, by season.

	Depth zone (m)			
	27–55	56–110	111–185	186–366
Winter	42.9	103.1	215.5	30.3
Spring	42.6	90.7	342.5	91.9
Autumn	853.3	352.8	377.2	66.5

Table 4

Diurnally adjusted, mean numbers-per-tow of *Loligo pealeii* from the three annual NEFSC bottom-trawl surveys, 1967–98, by area (NE=north of Hudson Canyon to the Gulf of Maine; MAB=south of Hudson Canyon to Cape Hatteras.

	Depth zone (m)			
	27–55	56–110	111–185	186–366
Winter NE	6.0	38.9	160.4	28.7
Winter MAB	83.5	396.2	510.7	36.0
Spring NE	2.3	24.7	259.5	81.4
Spring MAB	86.8	392.3	787.3	129.7
Autumn NE	644.2	365.9	392.8	72.4
Autumn MAB	1082.5	293.1	293.7	45.5

creased to peak values in deeper strata (111–185 m, greater than 10 times the catches in the shallowest strata), and were low in the deepest stratum (>185 m). Conversely, autumn survey catches were highest in the shallowest stratum (27–55 m) and lowest in the deepest stratum (>185 m). These patterns were also generally significant within both geographic regions (Table 4).

In the pairwise comparisons of the winter and spring surveys, catches were significantly greater at 111–185 m than in other depth zones. In the 27–55 m depth zone, au-

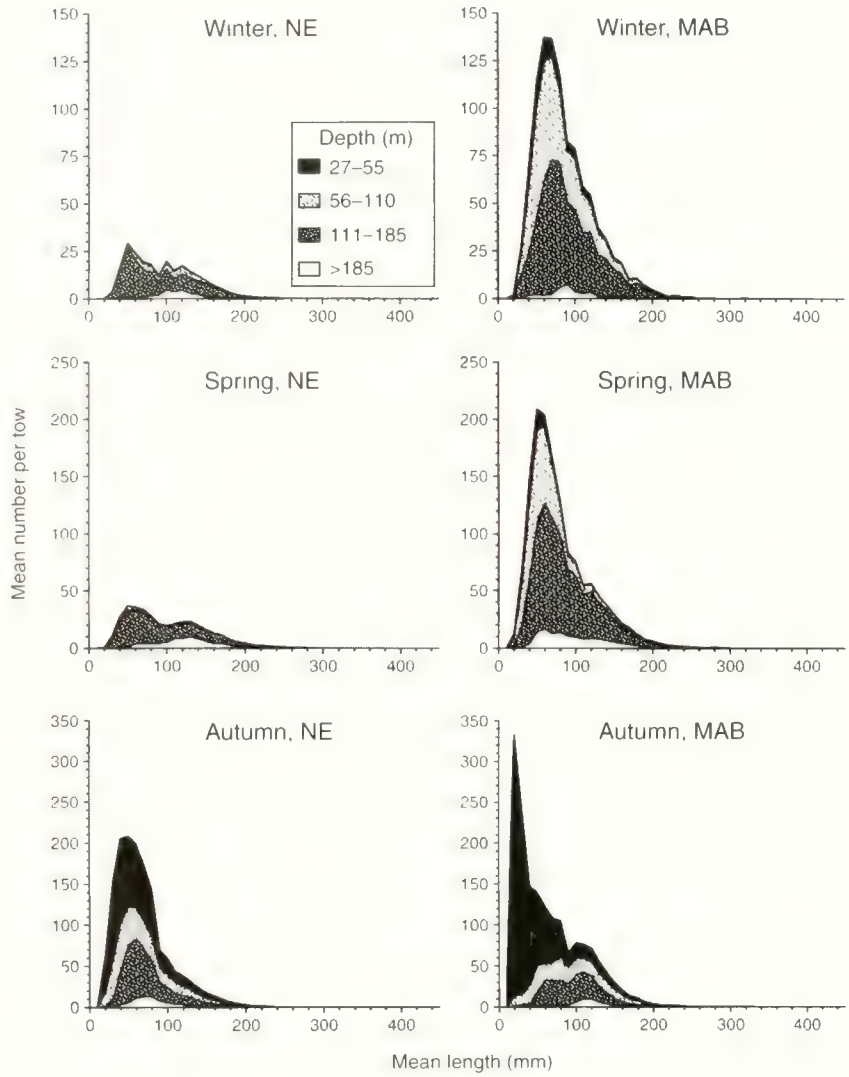

Figure 2

Diurnally adjusted mean numbers-per-tow of *Loligo pealei*, by length class, from Northeast Fisheries Science Center, National Marine Fisheries Service, surveys, by season, region, and depth. NE = north of Hudson Canyon to Gulf of Maine; MAB = south of Hudson Canyon to Cape Hatteras

tumn catches were considerably higher than in winter or spring. For all other depth zones and survey comparisons, the differences were not significant.

In the autumn survey, the proportion of small squid (≤50 mm ML) was highest at 27–55 m depths (over 50% of the sampled squid in that depth zone in the NE and almost 75% of the squid in that depth zone in the MAB, Table 5). Proportions of small squid at greater depths were considerably lower. These patterns show higher relative recruitment into the population in the shallow waters of the continental shelf in the autumn.

Similarly in the MAB during winter and spring, small squid form a higher proportion of squid sampled in the two shallowest depth zones than at greater depths. A higher percentage of small squid was present in spring than in winter, with over 60% of squid sampled in the MAB from 27–55 m being ≤50 mm ML. However, the highest proportion of small squid in the NE during winter and spring was at intermediate depths.

Biological analysis

The raw data of numbers sampled for each sex, length, and maturity stage are given in Table 6. For all seasons combined, the ML at 50% maturity during 1997–98 was approximately 200 mm ML for females and males (Table 7,

Table 5

The percentage of *Loligo pealeii* <50 mm ML in each depth zone, for each region and survey, and for the number of years for which these data were available (NE=north of Hudson Canyon to the Gulf of Maine; MAB=south of Hudson Canyon to Cape Hatteras).

	Winter		Spring		Autumn		Winter		Spring		Autumn	
Depth zone (m)	NE	(No. of years)	NE	(No. of years)	NE	(No. of years)	MAB	(No. of years)	MAB	(No. of years)	MAB	(No. of years)
27–55	3	6	17	20	51	31	33	7	64	30	73	31
56–110	11	7	40	31	19	31	27	7	48	31	27	31
111–185	27	7	24	31	31	31	14	7	22	31	9	31
186–366	7	3	2	31	14	30	10	3	14	31	2	31

Table 6

Numbers of *Loligo pealeii* measured, for each sex and maturity stage, from samples taken for biological analysis in 1997–99. Maturity was based on a four-stage scale for sexual maturity for each sex where 1 was immature and 4 was fully mature. ML = mantle length.

	Females					Males				
ML (mm)	Stage 1	Stage 2	Stage 3	Stage 4	Total ♀	Stage 1	Stage 2	Stage 3	Stage 4	Total ♂
30	1				1					
40	5				5	2				2
50	31	1			32	18				18
60	59	3	1		63	30	5		1	36
70	73	17	1		91	32	22	2	1	57
80	57	30	1	1	89	27	37	12	1	77
90	51	45	5		101	10	45	16	4	75
100	27	51	2	3	83	2	50	17	2	71
110	10	62	5	6	83	2	35	30	8	75
120	8	86	14	4	112	1	32	40	4	77
130	3	79	6	4	92		24	37	11	72
140	3	71	10	8	92		14	39	10	63
150	2	38	16	14	70		14	43	10	67
160		25	6	7	38		14	28	8	50
170		13	2	7	22		12	31	7	50
180		7	2	3	12		6	18	7	31
190		9	1	2	12		3	19	9	31
200		1		5	6			5	9	14
210		1	1	1	3		1	2	8	11
220			1	3	4		1	4	7	12
230							1		5	6
240							1	1	5	7
250							1	1	3	5
260									1	1
270				1	1				3	3
280									1	1
290									1	1
Total	330	539	74	69	1012	124	318	345	126	913

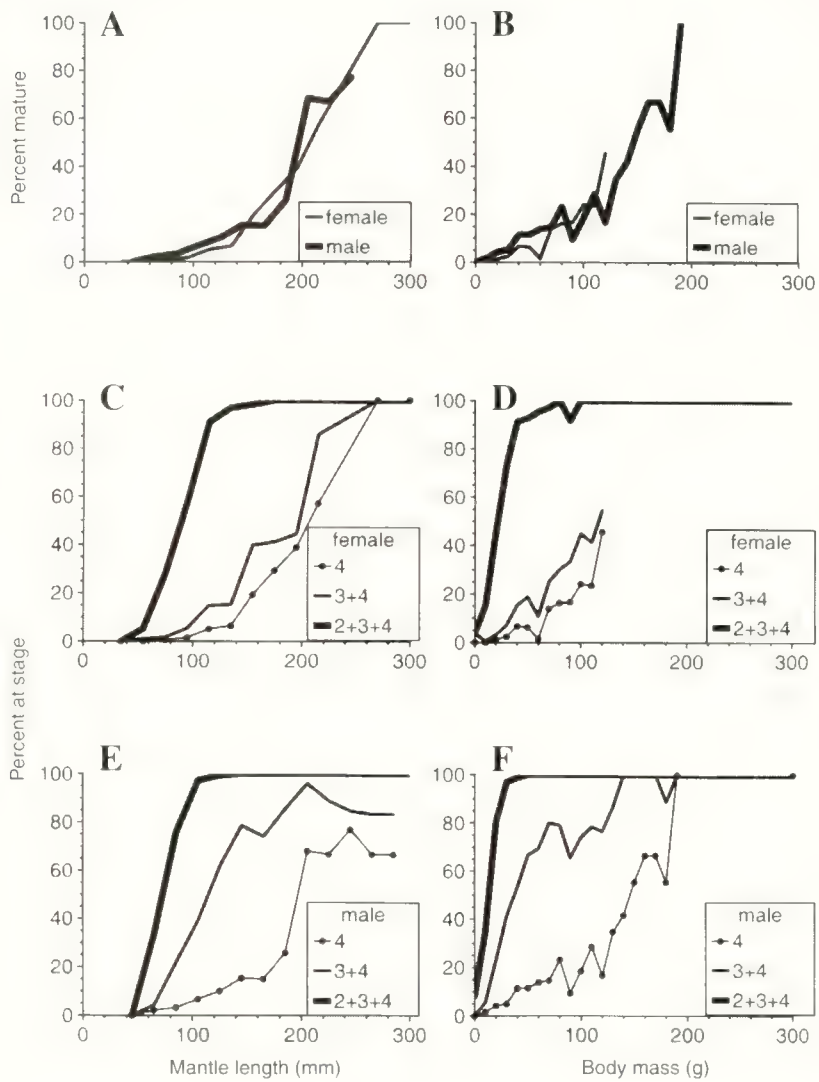

Figure 3

Percent mature of *Loligo pealeii* for dorsal mantle length (ML mm) (**A**) and wet body mass (BM g) (**B**). The percentage at each maturity stage is shown for female ML (**C**) and BM (**D**) and for male ML (**E**) and BM (**F**).

Table 7

Size at maturity for *Loligo pealeii* in mantle length (ML, mm) and body mass (BM, g), by sex. (—denotes a missing value).

	Female		Male	
Proportion mature	ML	BM	ML	BM
25%	166	111	184	113
50%	207	—	196	146
75%	238	—	211	184

Fig. 3, A and B). In terms of body mass, the size at 50% maturity for males was approximately 150 g, but, according to our samples, female maturity did not seem to be as closely associated with body mass (e.g. even squid in the heaviest size class were less than 50% mature).

In females, maturity stage 2 was reached at a relatively small size (Fig. 3, C and D). To reach stage 3 requires a considerable increase in length or body mass, whereas females in stage 4 are neither much longer, nor heavier than stage-3 females. Thus the transition from stage 3 to stage 4 (full maturity) takes place over a lesser period of somatic growth (and therefore possibly a shorter time period) than the transition from stage 2 to stage 3. In Macy's (1982) maturity stage notation, stage-3 females have no mature

Table 8

Diurnally adjusted, catch-weighted mean numbers-per-tow of *Loligo pealeii* sampled in each maturity stage. Maturity stages correspond to unsexed juveniles and a four-stage scale for sexual maturity for each sex where 1 was immature and 4 was fully mature (SOH: south of Cape Hatteras).

		Female				Male				
	Juvenile	Stage 1	Stage 2	Stage 3	Stage 4	Stage 1	Stage 2	Stage 3	Stage 4	Totals
Autumn	240.0	94.0	16.0	0.0	2.0	64.0	49.0	4.0	3.0	472.0
Winter	5.0	13.9	10.9	0.4	0.2	4.8	6.1	6.2	1.1	48.6
Spring plus SOH	26.3	12.7	10.0	2.3	1.4	5.4	5.0	5.0	2.4	70.5
Long Island Sound	436.0	0.0	52.0	378.0	176.0	161.0	0.0	196.0	144.0	1543.0
Commercial	0.0	5.0	155.0	0.0	0.0	8.0	198.0	331.0	15.0	712.0
Totals	707.3	125.6	243.9	380.7	179.6	243.2	258.1	542.2	165.5	2846.1

Table 9

Maturity patterns in *Loligo pealeii* (percentage of sample at each sex and stage derived from diurnally adjusted, catch-weighted mean numbers-per-tow. Maturity stages correspond to unsexed juveniles and a four stage scale for sexual maturity for each sex where 1 was immature and 4 was fully mature (SOH: south of Cape Hatteras).

		Female				Male			
	% juvenile	% stage 1	% stage 2	% stage 3	% stage 4	% stage 1	% stage 2	% stage 3	% stage 4
Autumn	50.7	20.0	3.4	0	0.5	13.6	10.3	0.9	0.6
Winter	10.3	28.7	22.4	0.7	0.4	9.8	12.5	12.7	2.2
Spring plus SOH	37.3	18.0	14.2	3.2	1.9	7.7	7.0	7.1	3.5
Long Island Sound	28.3	0	3.4	24.5	11.4	10.4	0	12.7	9.3
Commercial	0	0.7	21.8	0	0	1.1	27.8	46.5	2.1

oocytes (therefore they would not be considered to be close to maturity) and stage-4 females are fully mature.

In comparison, the transition of male squid (Fig. 3, E–F) from stage 2, to stage 3, to stage 4, seems more evenly spaced, with a more gradual development seen over the course of the maturation process. If anything, there seems to be a greater transition from stage 3 to stage 4, than from stage 2 to stage 3. The difference between stage-2 and stage-3 males is measured only as elongation of the testis in conjunction with a reduction in the ratio of mantle circumference to mantle length. In stage-4 males "elongate mature spermatophores are visible both in the Needham's sac and the penis." In subjective terms, stage 2 represents definitely immature, stage 3, maturing, and stage 4, fully mature males. Thus the rate at which full maturity is approached is very different between the sexes.

The raw data (numbers sampled in each size class, sex, and maturity stage) were then catch-weighted to be representative of the squid sampled in the different surveys and from commercial data. Catch-weighted proportions of female and male *L. pealeii* at each maturity stage are shown in Tables 8 and 9. In the autumn and spring surveys, and in the May Long Island Sound (LIS) samples, juvenile squid were the most abundant stage within the sampled population. In winter surveys the juveniles were one of the least abundant stages. Mature squid were never abundant in the NEFSC survey subsamples, nor in the inshore autumn (October) Massachusetts survey (combined with NEFSC data for autumn surveys). Most mature squid were seen in the LIS samples. In NEFSC surveys, the majority of both sexes were immature and stages 1 and 2. In LIS samples more squid were either stage 3 or 4 than immature. No mature females were observed in the commercial samples, although a small proportion of males were mature.

The catch-weighted mean ML for each maturity stage, by season, is given in Table 10. There was little difference between the size of juvenile squid between seasons. For both sexes, squid at stages 1, 2, and 3 were all longest in the autumn samples and shortest in the spring and LIS samples. Conversely, mature squid of both sexes (stage 4) were considerably larger in the spring than in autumn. In the LIS samples, mature female squid were the same size as in spring survey samples; mature male squid, on the other hand, were smaller than in the spring survey but larger than the autumn survey samples. Commercial samples showed a larger size for each maturity stage sampled.

Table 10

Mean dorsal mantle length (ML, mm) of *Loligo pealeii* for each sex and maturity stage (corresponding to unsexed juveniles and a four stage scale for sexual maturity for each sex where 1 was immature and 4 was fully mature), from diurnally adjusted, catch-weighted mean numbers-per-tow data (SOH: south of Cape Hatteras).

		Female				Male			
	Juvenile	Stage 1	Stage 2	Stage 3	Stage 4	Stage 1	Stage 2	Stage 3	Stage 4
Autumn	34	77	133		115	70	105	161	94
Winter	41	71	122	166	164	54	93	131	169
Spring plus SOH	37	58	90	122	139	61	83	114	143
Long Island Sound	47		90	79	138	70		83	109
Commercial		83	160			79	150	169	180

Table 11

Mean dorsal mantle length (ML, mm) and percentage of each sex for each sample of *Loligo pealeii* by depth stratum per survey. Derived from diurnally adjusted, catch-weighted tow data.

	Depth zone		Depth zone		Depth zone		Depth zone		Depth zone	
	<27 m	%	27–55 m	%	56–110 m	%	111–185 m	%	186–366 m	%
Autumn juvenile ML	32	73	29	72	47	58	48	5		0
Autumn female ML	67	13	87	13	95	25	92	21	123	68
Autumn male ML	67	14	105	15	111	17	80	74	118	27
Winter juvenile ML			42	10	39	4	39	5	46	5
Winter female ML			100	68	84	63	97	47	111	47
Winter male ML			105	22	93	33	97	48	131	48
Spring juvenile ML	35	42	43	3	37	54	40	3	43	1
Spring female ML	60	32	113	61	78	26	100	47	123	48
Spring male ML	59	25	129	36	90	18	104	49	136	51
Long Island Sound juvenile ML	47	28								
Long Island Sound female ML	97	39								
Long Island Sound male ML	86	33								
Commercial female ML							158	23		
Commercial male ML							161	78		

The distribution of the catch-weighted mean ML, by sex, by depth zone, for each season separately is shown in Table 11. For juvenile *L. pealeii*, in autumn, at 1–55 m depth, there was little difference in size at depth. In the 56–110 m depth zone, juveniles in autumn were considerably larger than at shallower depths. In winter, there was evidence for a slight increase in the size of juveniles with increasing depth. In spring survey samples, juveniles were similar in size across the depth range sampled.

Female and male *L. pealeii* were generally smaller in the shallowest depth zone (1–26 m, only sampled in autumn and spring surveys), and much larger at depths greater than 185 m, for each survey. There was no clear pattern for intermediate depths. In autumn surveys, squid were generally smaller at 27–55 m depth than in deeper water. In winter and spring, however, squid at this depth were longer than at 56–185 m. The LIS samples showed larger mean sizes for each group at <27 m depth than in autumn and spring samples.

In the autumn survey, squid of all maturity stages (except juveniles) were generally largest in the south (MAB) and smallest in the north (SNE and GOM, Table 12). Some of this distribution may have been an artifact of the sampling design because no squid were sampled in the MAB region in the 1–26 m depth zone, whereas this zone was sampled in the SNE, and was the only zone for which data were available for the GOM region.

In the winter survey, the general pattern was the reverse of that seen in the autumn. In this survey squid were generally smaller in the south (MAB) than in the

Table 12

Mean dorsal mantle length (ML, mm) by sex and maturity stage (corresponding to unsexed juveniles and a four-stage scale for sexual maturity for each sex, where 1 was immature and 4 was fully mature)of *Loligo pealeii* by region per survey. Derived from diurnally adjusted, catch-weighted mean numbers-per-tow data. MAB = Mid-Atlantic Bight; SNE = Georges Bank–Southern New England, north of Hudson Canyon; GOM = Gulf of Mexico; SOH = South of Cape Hatteras.

		Female				Male			
	Juvenile	Stage 1	Stage 2	Stage 3	Stage 4	Stage 1	Stage 2	Stage 3	Stage 4
Autumn MAB	23	98	132		162	69	120	172	170
Autumn SNE	38	71	130		85	69	102	147	96
Autumn GOM	33	68				65	69		71
Winter MAB	42	67	116	186	180	59	94	128	151
Winter SNE	50	80	127	148	159	52	94	134	171
Spring MAB	37	62	93	127	154	66	82	110	150
Spring SNE	41	51	95	132	151	54	88	125	183
Spring SOH		56	70	77	137	54	81	98	162
Long Island SNE	47		90	79	138	70		83	109
Commercial SNE		83	160			79	150	169	180

north (SNE only, no GOM samples were taken in the winter survey). The exception in winter were the few stage-3 and stage-4 females sampled.

In the spring survey, the same pattern as in the winter survey was observed; squid in the south were smaller than in the north. In the spring survey, samples available from south of Cape Hatteras (the limit of the MAB samples) followed the same trend because the observed mean sizes were smaller than the MAB samples. The exception to this were maturity-stage-1 squid.

Discussion

Survey analysis

The high proportion of small squid (≤50 mm ML) in the winter and spring surveys corroborated the occurrence of an early winter hatching event, documented from age data determined by squid statolith analysis (Brodziak and Macy, 1996; Macy[5]).

Mean numbers-per-tow of juvenile squid in the MAB were considerably higher than in the NE in all seasons surveyed. Recruitment of squid into the population was highest in autumn, but juvenile squid were distributed more widely over the continental shelf in the spring. Perhaps the MAB component of the *L. pealeii* stock was larger because it is more stable—a result of the higher proportion of squid recruited into the area each winter, spring, and autumn.

Murawski (1993) inferred a centering of the population in the MAB subject to the issue that portions of the stock are outside the area of the NEFSC surveys. Our data suggested that the area south of Cape Hatteras may play an important role in reproductive dynamics and recruitment to the population, suggesting that a considerable portion of the stock is south of the surveyed area, particularly during winter and spring. South of Cape Hatteras a second loliginid species, *L. plei*, is abundant (Roper et al., 1984). In our study, all *Loligo* specimens were examined carefully to ensure that only *L. pealeii* were measured and included in the biological analyses.

Diel differences in catches of *L. pealeii* have been observed in a number of studies (Summers, 1969; Serchuk and Rathjen, 1974; Roper and Young, 1975; Sissenwine and Bowman, 1978; Lange and Sissenwine, 1983; Lange and Waring, 1992), where catches were consistently higher in daytime than at night. To account for diel effects on minimum swept-area estimates of *L. pealeii* biomass and stock size, nighttime catches were adjusted to daytime equivalents by using the diel correction factors of Lange and Sissenwine (1983). However, these correction factors were not size specific. Brodziak and Hendrickson (1999) applied size-specific diel correction factors to squid from the autumn survey (1967–94), splitting the data into prerecruits (≤80 mm ML) and recruits (>80 mm ML). In the autumn surveys the nighttime catch of prerecruits was only 8.7% of the daytime catch. The nighttime catch of recruits was 34% of the daytime catch. These differences were attributed to the different feeding behavior of juvenile and adult squid, in that juvenile squid might need to undertake more vertical migrations at night to meet their higher metabolic requirements. In our present study, prerecruit nighttime catch differed to a lesser degree from the daytime catch in the winter and spring (65% in the winter surveys, and 51% in the spring surveys) than in the autumn. In the winter surveys, nighttime catches of recruits exceeded daytime catches by 31%. In spring, nighttime tows showed a lower catch of recruits, 72% of daytime values, than in winter. Patterns of diel differences reported in another study by Lange and Waring (1992) for spring catches were similar to those in our study. Their

reported autumn catches (Lange and Waring, 1992) were higher at night than in our study, but still lower than daytime catches.

The behavior of squid at both prerecruit and recruit sizes therefore appears to be different in the winter and spring than in the autumn. The prerecruit nighttime catch in winter and spring was half, or more than half of daytime catches, as opposed to 9% in autumn. For recruits, there was an even greater difference among seasons. In winter, almost 1.5 times as many squid were caught at night, than by day. In spring the nighttime catch was 72% of the daytime catch, twice the proportion of the autumn catch. Vovk (1978; 1985) and Maurer and Bowman (1985) have documented large changes in the diet of squid in different seasons, relating these changes in feeding activity and dietary preference to changes in the size composition of the squid population, movements of squid in search of food concentrations, seasonal abundance of prey, and environmental conditions that affect both prey and predator. Vovk (1985) noted that in autumn *L. pealeii* are daytime predators and do not feed extensively at night when they occur at shallow depths. In autumn, squid are more abundant near the seafloor by day (Brodziak and Hendrickson, 1999). Vovk (1985) also noted that feeding activity was generally low from December to April and related this to possible prey abundance. Perhaps the different diel behavior patterns of *L. pealeii* in winter and spring, when they appear to be more available to capture by bottom-trawls, are related to a lower prey abundance and a requirement for more time to be spent searching for prey. Some of these differences might be temperature related as well. In the autumn, with strong vertical stratification of the water column, there may be some physiological benefit for squid to move off the bottom at night into warmer waters. In winter and spring when there is no vertical stratification, no advantage is conferred by a strong diel migration as seen in the autumn.

Comparisons in performance and catchability of the two trawl nets used in the spring and autumn surveys (Yankee 36 and Yankee 41) have been conducted (Sissenwine and Bowman, 1978), but any differences in catchability were confounded by diel and vessel differences. In our study, we corrected for diel differences, and vessel differences were not found to be significant (NEFSC[8]).

Squid catches are more abundant in the autumn surveys than in winter and spring (Serchuk and Rathjen, 1974; Lange and Waring, 1992; Lange and Sissenwine[2]). This difference may be related to the recruitment of large numbers of small squid, present in shallow water, in autumn. Temperature, however, is a major factor limiting distribution. In winter and spring much of the continental shelf water is below the preferred temperature minimum for the species (ca. 8°C) (Summers, 1969; Serchuk and Rathjen, 1974; Murawski, 1993); therefore squid are apparently less abundant than in the autumn surveys when temperature is not a limiting factor. The greatest differences between autumn and spring or winter surveys are most apparent in the NE, where a large portion of the stock may be outside the surveyed area owing to temperature limits (e.g. off the shelf or south of Cape Hatteras). In the MAB there are few differences in catches between spring and autumn at depths deeper than 27–55 m. Spring numbers are higher than autumn numbers from 111 to 185 m. The patterns between autumn and winter catches are similar to each other at that depth. Catches are always lower in winter than in autumn, but the differences are only significant from 27–110 m depth.

In winter and spring surveys, catches were highest from 111 to 185 m, both in the NE and the MAB. Catches were higher, in both surveys, in the MAB than in the NE. These patterns also were observed for *L. pealeii* in survey analyses from 1967 to 1971 (Summers, 1969; Serchuk and Rathjen, 1974), from 1970 to 1977 (Lange, 1980), and from 1975 to 1986 (Lange and Waring, 1992). This finding may imply that geographic distribution is relatively stable for *L. pealeii*, during February and March, at least within the areas surveyed. In autumn surveys, Serchuk and Rathjen (1974), Lange (1980), and Lange and Waring (1992) also reported highest catches in the MAB. However, Serchuk and Rathjen (1974) showed a relatively higher abundance of squid taken from 56–110 m depth than that observed in our study, where mean numbers per tow in the depth zone 27–55 m were greater than three times higher than those in the zones 56–110 m and 111–185 m. The difference between the 27–55 m zone and deeper strata was less noticeable in the NE, although mean numbers-per-tow were almost twice as high in the 27–55 m zone. The differences may result from diurnal adjustments, or from the inclusion of more years of data in the survey database. Lange (1980) found mean numbers-per-tow in the NE autumn to be highest from 111 to 185 m depths.

Biological analysis

We found that squid mature at greater lengths than previously reported for *L. pealeii* (NEFSC[8]). Figure 3 (C–F) shows that using stage 3 or greater to indicate maturity may be an adequate proxy for females. For example, the size at which 50% of females are mature is 198 mm with stages 3 and 4, and 207 mm with only stage 4 (Fig. 3C). Such a proxy may be valuable for samples with few observations of stage-4 females (e.g. the body mass at 50% maturity is 120 g with stages 3 and 4 [Fig. 3D]).

For males, however, the size difference between stage 3 and stage 4 is considerable, and substantial somatic growth is required to develop from stage 3 to stage 4. Combining the two maturity stages in males is therefore unsupported biologically, and the combined data would underestimate size at 50% maturity.

That mature squid are largest in winter and smallest in autumn samples (and intermediate in size in the early [NEFSC] and late [LIS] spring) has been noted previously (Summers, 1971; Lange, 1980; Macy, 1980). Prior to the availability of age data for the species, the size differences at maturity were ascribed to different year class-

[8] NEFSC (Northeast Fisheries Science Center). 1996. Report of the 21st Northeast Regional Stock Assessment Workshop (SAW 21). Center Reference Document 90-05, 200 p. [Available from NEFSC, 166 Water St., Woods Hole, MA 02543.]

es (Summers, 1971; Lange, 1980; Macy 1980). The observation that immature squid are larger in autumn than in winter and spring was documented by Lange (1980) but not interpreted. Some of this variability might be explained as a function of temperature. If *L. pealeii* have a life-span of 9–12 months (Brodziak and Macy, 1996), then females that are mature in September–October samples would have hatched between November and January. Females that are mature in March would have hatched around May or June. Brodziak and Macy (1996) showed that squid hatched between November and April had a lower growth rate than those that hatched between May and October. Recent laboratory studies on small *L. pealeii* have indicated that squid grow significantly faster at higher temperatures (Hatfield et al., 2001), in accord with results described for other cephalopod species (*Octopus bimaculoides*—Forsythe and Hanlon, 1988; *L. forbesi*—Forsythe and Hanlon, 1989; *Sepia officinalis*—Forsythe et al., 1994). These laboratory studies also found that the effect of temperature on growth is most pronounced during the early life cycle of these cephalopods, nominally the first three months. If temperatures experienced by *L. pealeii* hatching in May and June are warmer than temperatures experienced by squid hatching from November to January, then the growth potential will be lower for winter-hatching squid (seen as mature squid in autumn surveys), resulting in the observed lower size at maturity in autumn versus winter and spring. The same phenomenon would explain the size differences of immature squid among seasons. The large immature squid caught in the autumn survey are probably the same squid that become the large, mature squid in the winter, spring, and LIS samples. The small immature squid in the spring are probably those squid which become the small mature squid seen in autumn survey samples. If the winter-hatching squid are from southern spawning events, then the temperature difference between winter-spawned and summer-spawned squid may not be very large. However, age data for *L. pealeii* show that growth rates are generally slower for winter hatched squid. Also, growth studies on *L. forbesi* have shown that a temperature difference of just 1°C can change growth rates of squid by 2% body weight/day and produce a threefold difference in weight at 90 days after hatching (Forsythe and Hanlon, 1989).

The high numbers of juvenile squid in the autumn survey were from protracted spawning in inshore waters some 4–5 months previously (documented since Verrill [1882] first reported inshore spawning). The high proportion in spring therefore reflects a period of spawning, possibly also some 4–5 months earlier, around September or October of the previous year. Juvenile squid in winter and spring survey samples denote the presence of a hatching component other than the main inshore autumn component. The high proportion observed in LIS (May) samples probably reflects an extended winter–spring spawning period because squid of the size found in Long Island Sound in May could not have been the result of that season's inshore spawning. The inshore spawning season does not usually begin until late April and incubation time may require up to 4 weeks at the temperatures at that time of year (27 days at 12°C, McMahon and Summers, 1971). Brodziak and Macy (1996) showed a pattern of year-round hatching, which is consistent with the patterns suggested by our data.

Summers (1969), Serchuk and Rathjen (1974), and Brodziak and Hendrickson (1999) all reported an increase in size of *L. pealeii* with increasing depth. We found the smallest squid in the shallowest water and the largest squid in the deepest water, confirming that nearshore waters of the continental shelf are a preferred habitat for juvenile *L. pealeii* during the autumn (as described by Brodziak and Hendrickson [1999]). The pattern of ontogenetic descent exhibited by other loliginid species (*L. vulgaris*—Worms, 1983; *L. gahi*—Hatfield et al., 1990; *L. vulgaris reynaudii*—Augustyn et al., 1992) is consistent in *L. pealeii*, but less marked at intermediate depths.

In winter and spring, mean length is generally higher in the NE and lower in the MAB. In autumn, mean length is generally lower in the NE and higher in the MAB. Lange (1980) showed a similar pattern for immature females from the autumn survey. Males, however, showed the opposite pattern. Lange's (1980) winter and spring survey data showed the same pattern as our study for immature females and all males, except the fully mature squid.

Commercial samples from early winter (December and January) contained no mature female squid that might produce the winter hatching component evident from age data and aggregated survey length-frequency distributions. Egg masses are only found consistently in one small offshore area (off Chesapeake Bay) by commercial fishermen in the early winter (see Fig. 4). However, the commercial samples were from the southern edge of Georges Bank, and the survey data suggest that the winter recruitment originates from the southern part of the MAB. The scarcity of mature squid in NEFSC survey samples suggests that sampling did not occur consistently in the right areas or seasons to identify major spawning peaks. Whitaker (1978) documented that about 40% of males were fully mature in January and February in the region south of Cape Hatteras, off the coast of South Carolina. There was a large proportion of mature squid in samples from March and April, with 74% of females and 56% of males fully mature. There is evidence for both spawning and hatching in the SNE from March to April; as in 1999, egg masses were caught incidentally from northeast of Hudson Canyon and up towards the southern flank of Georges Bank, at depths of about 200 m, from mid-March to late April (Stommell[9]). In the 1998 Massachusetts spring survey, in mid-May, a high abundance of small squid, about 30 mm ML, were caught south of Martha's Vineyard, at depths of <27 m (senior author, personal obs.). These observations suggest that spawning is probably protracted, from early to late winter, and early winter spawning is more dominant in the southern end of the U.S. continental shelf. Thus, the available fishery-dependent samples may not be indicative of the population. The information on age and maturity in Brodziak and Macy (1996) was derived from

[9] Stommell, M. 1999. Personal. commun. FV *Nobska*, Woods Hole, MA 02543.

data collected from the winter fishery, most of which occurs north of the MAB region. A more structured design is required to address some of these issues. The entire size and maturity stage range needs to be sampled across the geographic range of each survey and these data should be augmented with opportunistic sampling outside the area or time frame in which the surveys are carried out.

In summary, results from these two studies complement each other to reveal patterns of reproductive dynamics for *L. pealeii* that have been suggested previously in other studies but that have never thoroughly been investigated. The high frequency of small squid present in spring survey catches indicates that winter spawning is indeed an important component of reproduction for the population, and biological analyses suggest that this winter spawning occurs primarily south of Cape Hatteras, rather than in the vicinity of the offshore submarine canyons along the edge of the northeastern U.S. continental shelf, from Hudson Canyon up to Georges Bank.

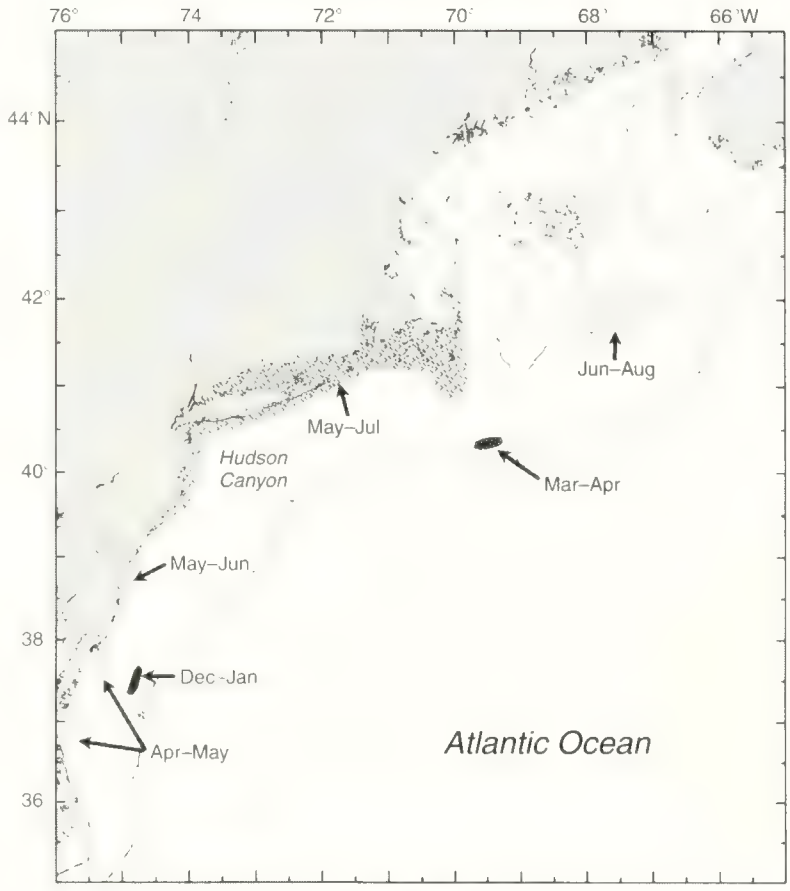

Figure 4

Persistent spawning areas and seasons for *Loligo pealeii*, as indicated from incidental catches of eggs in commercial squid trawls.

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Age and size composition, growth rate, reproductive biology, and habitats of the West Australian dhufish (*Glaucosoma hebraicum*) and their relevance to the management of this species

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Abstract—Samples of the commercially and recreationally important West Australian dhufish (*Glaucosoma hebraicum*) were obtained from the lower west coast of Australia by a variety of methods. Fish <300 mm TL were caught over flat, hard substrata and low-lying limestone reefs, whereas larger fish were caught over larger limestone and coral reef formations. Maximum total lengths, weights, and ages were 981 mm, 15.3 kg, and 39 years, respectively, for females and 1120 mm, 23.2 kg, and 41 years, respectively, for males. The von Bertalanffy growth curves for females and males were significantly different. The values for L_∞, k, and t_0 in the von Bertalanffy growth equations were 929 mm, 0.111/year, and –0.141 years, respectively, for females, and 1025 mm, 0.111/year, and –0.052 years, respectively, for males. Preliminary estimates of total mortality indicated that *G. hebraicum* is now subjected to a level of fishing pressure that must be of concern to fishery managers. *Glaucosoma hebraicum*, which spawns between November and April and predominantly between December and March, breeds at a wide range of depths and is a multiple spawner. The L_{50}'s for females and males at first maturity, i.e. 301 and 320 mm, respectively, were attained by about the end of the third year of life and are well below the minimum legal length (MLL) of 500 mm. Because females and males did not reach the MLL until the end of their seventh and sixth years of life, respectively, they would have had, on average, the opportunity of spawning during four and three spawning seasons, respectively, before they reached the MLL. However, because *G. hebraicum* caught in water depths >40 m typically die upon release, a MLL is of limited use for conserving this species. Alternative approaches, such as restricting fishing activity in highly fished areas, reducing daily bag limits for recreational fishermen, introducing quotas or revising specific details of certain commercial hand-line licences (or doing both) are more likely to provide effective conservation measures.

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The West Australian dhufish (*Glaucosoma hebraicum*), also known as the Westralian jewfish (McKay, 1997), is one of the most commercially valuable and recreationally sought after finfish in Western Australia (Sudmeyer et al.[1]). This species is confined to southwestern Australia, where its distribution ranges southwards from Shark Bay at 26°00′S, 113°00′E down the west coast and then eastwards along the south coast to the Recherche Archipelago at 34°10′S, 122°15′E (Hutchins and Thompson, 1995). *Glaucosoma hebraicum* is one of four members of the monogeneric family Glaucosomatidae, which also includes the pearl perch (*Glaucosoma scapulare*) that is fished commercially and recreationally in eastern Australia (McKay, 1997).

Despite the high quality of the flesh of *Glaucosoma* species and the commercial and recreational importance of *G. hebraicum* in particular, there are no refereed papers on the biology of any species in this genus. Furthermore, the results of undergraduate studies on the biology of *G. hebraicum*, which were collated by Sudmeyer et al.,[1] included estimates of age that were based on the number of growth zones in whole otoliths, an approach that would almost certainly have underestimated the age of many older fish (see "Results" section).

Numerous commercial and recreational fishermen report that they now fish much farther offshore in order to obtain catches of dhufish comparable with those they had previously been able to obtain from nearer the coast. This consistent circumstantial evidence strongly suggests that the abundance of *G. hebraicum* in more inshore waters has declined in recent years and that this is particularly the case in areas near the city of Perth where this species has been targeted by recreational fishing crews. The indications that the abundance of dhufish in nearshore waters was declining led the Australian Fisheries Research and Development Corporation to fund the current study, with a view to producing biological data for managing *G. hebraicum*.

During the present study, we first determined whether the otoliths of *G. hebraicum* had to be sectioned to detect all of their opaque zones and we then validated that these opaque zones are formed annually and could thus be used to age this species. As accurate estimates of the age of a fish are dependent on a reliable birth date, the trends exhibited by reproductive variables were used to estimate the duration of the spawning period and, in particular, when spawning activity peaked. The age of each fish was then determined and the resulting length-at-age

[1] Sudmeyer, J. E., D. A. Hancock, and R. C. J. Lenanton. 1992. Synopsis of Westralian jewfish (*Glaucosoma hebraicum*) (Richardson, 1845) (Pisces: Glaucosomatidae). Fisheries Research Report 96, Western Australian Marine Research Laboratory, Fisheries Western Australia, PO Box 20, North Beach 6020, Western Australia.

data employed to determine the age compositions and growth rates of female and male *G. hebraicum*. The reproductive variables were also used to help ascertain where *G. hebraicum* spawns and whether this species is a multiple spawner *sensu* deVlaming (1983), i.e. whether individual females release eggs on more than one occasion in a spawning season. The lengths of both sexes at first maturity were calculated to determine whether they lay below the minimum legal length (MLL) of 500 mm and were thus appropriate for helping to conserve this species. The ages at which females and males mature were also determined in order to elucidate whether fish might spawn in one or more spawning seasons before they attain the MLL. Attempts were also made to ascertain the types of habitat occupied by *G. hebraicum* at different stages during its life cycle and to obtain preliminary mortality estimates which could be used as an indicator of whether this species is being lightly or heavily fished. Finally, the data collected during this study were used to discuss ways in which the fishery for *G. hebraicum* might be managed most appropriately in the future.

Materials and methods

Glaucosoma hebraicum, that were less than the MLL of 500 mm total length (TL), were collected between May 1996 and June 1999 by commercial trawls, hand-lines, and a recreational spear diver under a research collection permit issued by Fisheries Western Australia—the government agency responsible for managing the fishery for this species. Filleted carcasses of *G. hebraicum* ≥500 mm TL, together with their gonads, were obtained monthly between May 1996 and April 1998 from commercial fish-processing plants and weigh-ins at local recreational fishing club competitions. These fish had been caught by commercial or recreational rod and hand-lines along the lower west coast of Australia between Mandurah (32°32′S) and the Houtman Abroholos (28°35′S), i.e. within that part of the distribution of *G. hebraicum* where this species is considered to be most abundant and is most heavily fished.

The total length of each fish was measured to the nearest 1 mm and the weight of each fish <500 mm was weighed to the nearest 1 g. The weights of 334 females and 442 males ≥500 mm TL were weighed to the nearest 10 g prior to filleting. The relationship between total length (L) in mm and total wet weight (W) in g of each sex was

$$\text{Females} \quad \log W = \log 0.0000417 + 2.859 \log L \quad (n=486,\ r^2=0.995)$$

$$\text{Males} \quad \log W = \log 0.0000322 + 2.898 \log L \quad (n=572,\ r^2=0.995).$$

These relationships were then used to estimate the weights of the female and male fish that had been filleted but not weighed. Note that all of the logarithm values recorded in this paper are natural logarithms.

On several occasions, a video camera, attached by cable to a television monitor and video recorder, was lowered over the substrata during commerical hand-line fishing for dhufish. Video footage of the substrate over which dhufish were caught was later examined to determine the types of habitat occupied by this species.

Age determination

The two sagittal otoliths of each fish were removed, cleaned, dried, and then stored in paper envelopes. All sagittal otoliths were sectioned, except for those which, when placed in methyl salicylate and examined microscopically under reflected light against a black background, could clearly be seen to possess either no opaque zones or only a single opaque zone. However, because the opaque zones in the whole otoliths of large fish were so numerous and closely spaced that they were often difficult to distinguish from one another and because previous estimates of the age of dhufish were based on counts of opaque zones in whole otoliths (Sudmeyer et al.[1]), the number of opaque zones visible in 100 otoliths, obtained from a wide size range of fish, were compared prior to and after sectioning to ascertain whether sectioning increased one's ability to detect the opaque zones.

For sectioning, the otoliths were mounted in clear epoxy resin and cut into 500 µm sections with a low-speed diamond saw (Buehler). The sections were cleaned and mounted on slides with DePX mounting medium and examined under reflected light with a dissecting microscope attached to a video camera (Panasonic WV-CD20). The image was analyzed by using the computer imaging package Optimas 5 (Optimas, 1995). The number of opaque zones in each otolith was always counted twice and on different days and without knowledge of either the date of capture or the size of the fish from which the otolith came, and also, in those cases where the two counts differed, on a third occasion. Although the number of times that a third count did not agree with either of the two previous counts was negligible for otoliths with less than 15 opaque zones, such disagreement increased to ca. 10% for otoliths with 15–25 opaque zones and ca. 30% for those with more than 25 opaque zones. When a third count was necessary and was not the same as either of the two previous counts, further counts were made until successive counts did not differ by more than two opaque zones. On such occasions, the final count was recorded.

An independent reader counted the number of opaque zones on 110 otoliths from a wide size range of fish. Eighty four percent of the counts of the number of opaque zones made by this independent reader were the same as those of the senior author for 50 sectioned otoliths that had been judged by the senior author to have up to 10 such zones and, in those cases where there were discrepancies, the differences were never more than one opaque zone. Eighty percent of the counts made by the independent reader of the number of opaque zones on 50 sectioned otoliths recorded as possessing between 11 and 25 such zones by the senior author were the same or differed by only one from those of the senior author and, where there were discrepancies, these rarely exceeded three opaque zones. In the case of ten otoliths with >25 opaque zones, the maximum dis-

crepancy between the counts recorded by the independent reader and the senior author was five. After consultation, it was agreed that, in many of the cases where the counts differed by one opaque zone, the independent reader had failed to discern the outermost opaque zone at the periphery of the otoliths. Moreover, the extent of any discrepancy between the counts of the independent reader and the senior author declined if the independent reader continued to recount the number of opaque zones on the otoliths.

Validation that the opaque zones in the otoliths of *G. hebraicum* are formed annually was carried out by analyzing the trends exhibited throughout the year by the marginal increments on whole otoliths, when only one opaque zone was present, and on sectioned otoliths when two or more opaque zones were present. For this purpose, the marginal increment on each otolith, i.e. the distance between the outer edge of the single or outermost opaque zone and the edge of the otolith, was expressed either as a proportion of the distance between the primordium and the outer edge of the opaque zone, when only one opaque zone was present, or as a proportion of the distance between the outer edges of the two outermost opaque zones, when two or more opaque zones were present. Each of the above requisite distances was measured perpendicular to the opaque zone(s) and without knowledge of the date of capture of the fish and was recorded to the nearest 0.01 mm by using Optimas 5. The values for the marginal increments were separated into groups according to the number of opaque zones on the otoliths, i.e. 1, 2–5, 6–8, 9–11 etc., after which the values for each of those groups in each corresponding month of the year between May 1996 and April 1998 were pooled.

Von Bertalanffy growth equations

The time when spawning peaked was estimated from the trends exhibited throughout the year by gonadosomatic indices, gonadal maturity stages, and pattern of oocyte development. This time was considered to correspond to the birth date of *G. hebraicum* and could thus be used, in combination with the number of opaque zones on the otolith and the time when the annulus becomes delineated on the otolith, to determine the age of individual fish on their date of capture. Because the sex of fish <150 mm could not be determined, the lengths-at-age of these small fish were randomly allocated in equal numbers to the data sets for female and male fish used for constructing the growth curves.

Assumptions are made concerning the distribution of errors when fitting von Bertalanffy growth curves to length-at-age data. Kimura (1980) discussed the implications of the following three assumptions, namely that 1) the individual lengths-at-age have a constant variance, 2) the mean lengths-at-age have a constant variance and 3) the variance of the lengths-at-age is dependent on age. The assumption most frequently adopted in growth studies is that the individual lengths-at-age have a constant variance. As discussed by Kimura (1980), different assumptions regarding the error variance require modifications to the objective function to ensure that the parameters are estimated accurately and that any comparisons between growth curves, that are based on the likelihood ratio, are appropriate.

A von Bertalanffy growth equation was fitted to the lengths-at-age of female and male fish with the traditional assumptions that the lengths-at-age are normally distributed around the values predicted from the growth equation and that the variance of this distribution is constant for each sex over all ages. However, visual examination of the residuals for each curve suggested that it was not appropriate to make the latter assumption. Further study showed that the variance of the residuals is approximately proportional to the age of the fish, as above in assumption 3 of Kimura (1980). Thus, the von Bertalanffy growth equation was fitted to the length-at-age data for each sex by using the assumption that the residuals were normally distributed, where the variance of this distribution was proportional to age but dependent on sex. That is,

$$\hat{L}_j = L_\infty \left\{1 - \exp\left[-k(t_j - t_0)\right]\right\}$$

$$\text{and } L_j = \hat{L}_j + \varepsilon_j,$$

where, for each sex, L_j = the observed length at age;
$\hat{L}_j$ = the estimated length-at-age;
t_j = the age; and
ε_j = the error associated with the jth fish.

For the growth curves for females and males, L_∞ is the mean asymptotic length predicted by the equation, k is the growth coefficient, and t_0 is the hypothetical age at which fish would have zero length if growth had followed that predicted by the equation. The errors are assumed to be normally distributed, such that $\varepsilon_j \sim N(0, c_s t_j)$, where c_s is the constant of proportionality between the variance of the residuals and age for fish of sex s. The growth equations were fitted to the observed length-at-age data for both sexes by maximizing the log-likelihood of the data. The log-likelihood for the combination of male and female fish, λ, may be written as

$$\lambda = \lambda_M + \lambda_F$$

where λ_s = the log-likelihood associated with females or males and may be calculated as

$$\lambda_s = -\frac{n_s}{2}\log(2\pi) - \frac{1}{2}\sum_{j=1}^{n}\log(c_s t_j) - \frac{1}{2c_s}\sum_{j=1}^{n}\left\{\frac{(L_j - \hat{L}_j)^2}{t_j}\right\},$$

and n_s = the number of fish of that sex in the length-at-age data.

The maximum likelihood estimate of c_s for each sex is given by

$$c_s = \frac{1}{n_s}\sum_{j=1}^{n}\left\{\frac{(L_j - \hat{L}_j)^2}{t_j}\right\}.$$

The SOLVER routine in Microsoft EXCEL (Microsoft Corp., 2000) was used to estimate the parameters that

would maximize the log-likelihood function, by fitting the equations to the combined set of length-at–age data for both females and males.

The growth curves for the fish of each sex were compared following the likelihood ratio method described by Kimura (1980) and Cerrato (1990). The test of the likelihood ratio, Λ, that was applied was to reject the null hypothesis Ω (that there was no difference between the curves) at the α level of significance when

$$\Lambda^{2/n} > \left(1 + \frac{q}{f_M + f_F} F^{\alpha}_{q(f_M+f_F)}\right),$$

where $\Lambda = \left(\frac{\hat{\sigma}^2_{M\omega}}{\hat{\sigma}^2_{M\Omega}}\right)^{n_M/2} \left(\frac{\hat{\sigma}^2_{F\omega}}{\hat{\sigma}^2_{F\Omega}}\right)^{n_F/2}$

and where $n = n_M + n_F$;
$f = n - 3$; and
q = the number of linear constraints of the form $\theta_M = \theta_F$, where θ is one of the parameters L_∞, k, t_0.
M and F = males and females, respectively.

This test was developed by Gallant (1975), as described by Cerrato (1990).

The growth curves were fitted under all possible parameter sets, and the best of both the 4- and 5-parameter, models, i.e. those that maximized the log-likelihood, were selected. The resulting 3-, 4- and 5-parameter models were compared with the 6-parameter model by using the above test to determine which of these three models, w, was of minimum complexity and not significantly different from the 6-parameter model Ω. The model selected on the basis of these tests was the simplest model that, in the statistical sense, provided the best description of the data.

Reproductive biology

The gonads of each fish that could be sexed macroscopically were removed and weighed to the nearest 0.01 g. Each gonad was allocated to a maturity stage, based on the scheme of Laevastu (1965), but which, in the case of females, also took into account the histological characteristics of the ovaries (see "Results" section).

The percentage contributions made by the different gonadal stages in sequential 50-mm length intervals were calculated for both female and male *G. hebraicum*. The lengths at which 50% of female and male *G. hebraicum* reach sexual maturity (L_{50}) were determined by fitting the logistic curve to the percentage of female and male fish which, during the spawning period, possessed gonads at stages III to VIII (see "Results" section for rationale for using these six stages for this purpose). The logistic curve was fitted by employing a nonlinear technique (Saila et al., 1988) and by using a routine statistical method provided in SPSS (SPSS Inc., 1988). The logistic equation is $P_L = 1/(1 + e^{(a+bL)})$, where P_L is the proportion of fish with mature gonads at the mid-point of the length class, L, and a and b are constants. The L_{50} for each sex was derived from the equation $L_{50} = \frac{a}{b}$. The ages at which 50% of females and males reached maturity, i.e. the A_{50}, were estimated, as follows, from the inverse von Bertalanffy growth equations for the two sexes (see Stergiou, 1999):

$$A_{50} - t_0 \left(\frac{1}{k}\right) \log\left(1 - \frac{L_{50}}{L}\right).$$

Gonadosomatic indices (GSIs) of females and males $\geq L_{50}$ at first maturity were determined from the equation

$$W1/W2 \times 100,$$

where $W1$ = wet weight of the gonad; and
$W2$ = wet weight of the whole fish.

Mortality

Preliminary analysis of catch curves demonstrated that the mortality estimates derived for commercially and recreationally caught fish that were greater than the MLL of 500 mm and eight years old and thus fully recruited (see "Results" section) were similar. Thus, the data from the commercial and recreational samples were pooled for estimating mortality. An estimate of the instantaneous coefficient of natural mortality, M, was determined from the von Bertalanffy growth coefficient, k, with the regression equation developed by Ralston (1987), i.e. $M = 0.0189 + 2.06k$. The instantaneous coefficient of total mortality, Z, was determined by maximizing the likelihood, when fitting the estimated age composition resulting from that mortality to the observed age composition data for those dhufish that were greater than the MLL of 500 mm and eight years old. In order to assess whether the observed age composition data reflected decreasing levels of total mortality in earlier years, the catch curve analysis was repeated with different initial ages, ranging from 10 to 30 years. Values of Z were also estimated by using the observed maximum age (t_{max}) for the sampled dhufish, employing both the regression equation reported for fish by Hoenig (1983), i.e.

$$\log(Z) = 1.46 - 1.01 \log(t_{max}),$$

and the equation for the expected value of the maximum age in a sample of size n, i.e.

$$E(t_{max}) = \frac{1}{Z} \sum_{i=1}^{n} \frac{1}{i} + t_c,$$

where t_c = the age at which fish become fully recruited to the fishery (Johnson and Kotz, 1970, p. 216, as reported by Hoenig, 1983).

Results

Habitats of *Glaucosoma hebraicum*

Glaucosoma hebraicum <150 mm TL and <14 months old were caught regularly by trawlers offshore in water

depths of 27 to 33 m. The depth sounder indicated that these small *G. hebraicum* were most consistently caught over hard substrate that lay adjacent to reefs—a conclusion later confirmed by video footage. Although a considerable amount of effort and a variety of techniques were employed in attempts to catch fish with lengths of 150–300 mm, only a small number of fish of this size were collected. However, a few *G. hebraicum* of this length class were caught by an experienced spearfisher while diving over low-lying reefs with rock ledges <30 cm high. Large numbers of dhufish >300 mm in length were obtained from rod and handline fishermen who were fishing in waters that were shown by video camera and commercial echo sounders to be located over limestone and coral reef formations and, in particular, where the "drop-offs" (reef edges) were two or more metres in height.

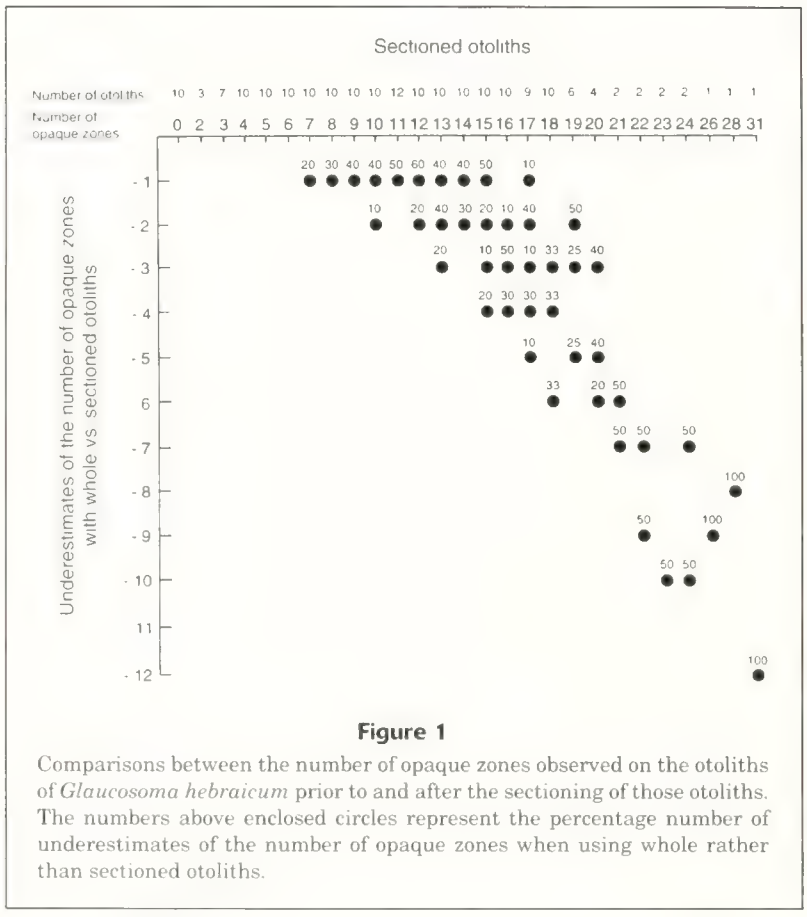

Figure 1

Comparisons between the number of opaque zones observed on the otoliths of *Glaucosoma hebraicum* prior to and after the sectioning of those otoliths. The numbers above enclosed circles represent the percentage number of underestimates of the number of opaque zones when using whole rather than sectioned otoliths.

Comparisons between number of opaque zones visible in whole and sectioned otoliths

The number of opaque zones observed in each sectioned otolith, in which up to six such zones could be seen, was the same as those visible on the same otolith prior to sectioning (Fig. 1). However, this frequently did not apply when a greater number of opaque zones were present. Furthermore, where such discrepancies occurred, the differences between the number of opaque zones detected prior to and after sectioning rose as the number of opaque zones increased. In all cases where there were discrepancies, the number of opaque zones detected after sectioning was greater than prior to sectioning. Underestimates of the number of growth zones with whole otoliths, based on comparisons with those detected in sectioned otoliths, rose from one in whole otoliths with seven to nine opaque zones to between one and seven in those with 10–21 opaque zones (Fig. 1). In otoliths with a large number of opaque zones, the differences sometimes exceeded eight and for one such otolith was as high as twelve. These comparisons demonstrated that, for validation that opaque zones are formed annually and that these zones can thus be used for aging *G. hebraicum*, experiments should be conducted on sectioned otoliths.

Validation that opaque zones are formed annually

The mean monthly marginal increments on sectioned otoliths with 2 to 16 or more opaque zones rose from a low level in January to a maximum in September, before declining precipitously to a minimum in October and then rising slightly in December (Fig. 2). They thus reached high levels in early spring, before declining markedly in mid-spring, as the outermost opaque zone became delineated through the formation of a new translucent zone, and then increased progressively in the ensuing months as the translucent region increased in width. Although fish possessing otoliths with one opaque zone were not caught in all months, the trends exhibited by the mean monthly marginal increments for those months when such fish were caught were consistent with those exhibited by otoliths with a larger number of opaque zones.

Because the mean monthly marginal increment rose and declined only once during the year, irrespective of the number of opaque zones in the otolith, a single opaque zone is laid down in the otoliths of *G. hebraicum* each year. The number of opaque zones in sectioned otoliths can thus be used, in conjunction with the birth date of *G. hebraicum* and the month when the opaque zone(s) become delineated, to age this species.

Growth of *Glaucosoma hebraicum*

Because the trends exhibited by the GSIs and stages in gonadal maturation and oocyte development demonstrated that the spawning of *G. hebraicum* peaked from late January through early February, this species was assigned a birth date of 1 February. Age 0+ *G. hebraicum* were first caught by trawling over hard substrate in April and May, when their lengths ranged from 57 to 81 mm (Fig. 3). However, substantial numbers of the 0+ age class were not

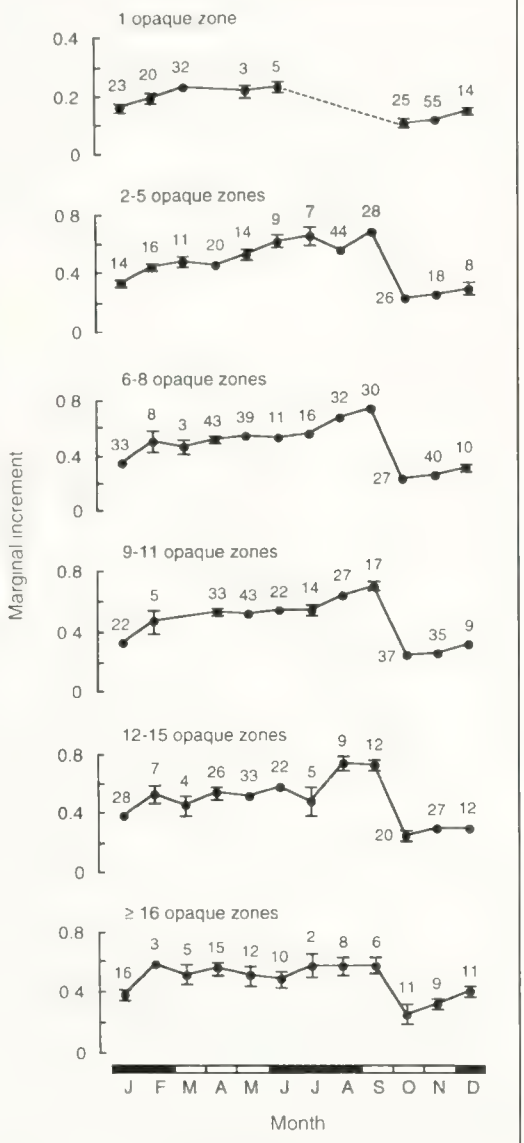

Figure 2

Mean monthly marginal increments ±1SE for sagittal otoliths of *Glaucosoma hebraicum*. Sample size is given for each month. In this Figure and Figure 5, the closed rectangles on the horizontal axis refer to summer and winter months and the open rectangles to autumn and spring months.

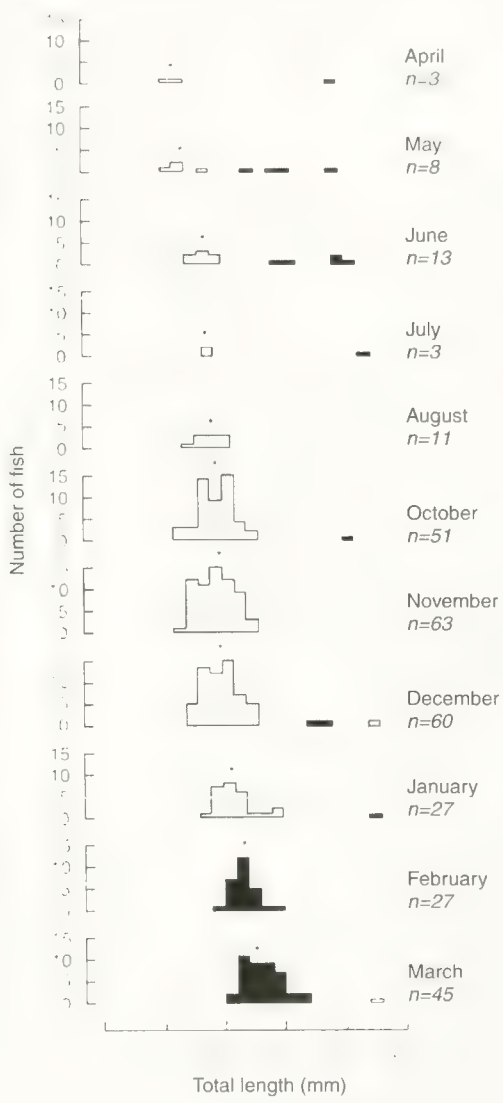

Figure 3

Length-frequency distributions for *Glaucosoma hebraicum* caught by trawling along the lower west coast of Australia by using data for corresponding months in the period May 1996 to June 1999. *denotes mean lengths of 0+ and early 1+ fish. Histograms in gray refer to 0+ fish, and those in black and white refer to 1+ and 2+ fish, respectively.

caught until October, presumably reflecting the time typically required for the 0+ age class to be recruited into these areas from those in which spawning occurs. The mean length of the 0+ age class had reached 95 mm by October, in which month the first opaque zone became delineated on the otoliths, and 108 mm by January, when fish were approaching the end of their first year of life. The mean length of the corresponding cohort, now early 1+, was 127 mm in March, after which month the number of 1+ fish caught in trawl samples declined markedly (Fig. 3).

The best of the 4- and 5-parameter growth curves were selected as the models with the largest log-likelihood at that level of model complexity. The best 4-parameter model was the curve that assumed different asymptotic lengths for the sexes, and the best 5-parameter model was that which assumed that the growth coefficients were equal.

Comparisons between the curves demonstrated that the model that assumed common growth coefficients for females and males was not significantly different ($P>0.05$) from the more complex model, which assumed that all

parameters of the growth curves differed between the sexes. For this curve, the parameters L_∞, k, and t_0 and their 95% confidence limits were estimated to be 929 (908 to 949) mm, 0.111 (0.107 to 0.116)/year, and –0.141 (–0.183 to –0.100) years, respectively, for females, and to be 1025 (1003 to 1048) mm, 0.111 (0.107 to 0.116)/year, and –0.052 (–0.088 to –0.016) years, respectively, for males. The growth curves for females and males were significantly different (P<0.001), with the asymptotic lengths having the most influence on the difference between the sexes. The estimated constant of proportionality between the variance of the residuals and age were 363 for females and 320 for males.

The von Bertalanffy growth curves demonstrated that females grow slightly slower than males. Thus, at ages 2 to 5, females had reached lengths of 196, 273, 342, and 404 mm, compared with 209, 294, 371, and 440 mm for males. By the time *G. hebraicum* had attained 10, 15, and 20 years, the females had reached ca. 628, 756, and 830 mm, respectively, and the males had reached ca. 689, 832, and 914 mm, respectively (Fig. 4). The maximum ages recorded for females and males were 39 and 41 years, respectively, and the maximum total lengths of females and males were 981 mm (=ca. 15.3 kg) and 1120 mm (=ca. 23.2 kg), respectively. The ages at which female and male *G. hebraicum* reach the minimum legal length for capture (500 mm TL) were 7.0 and 6.0 years, respectively.

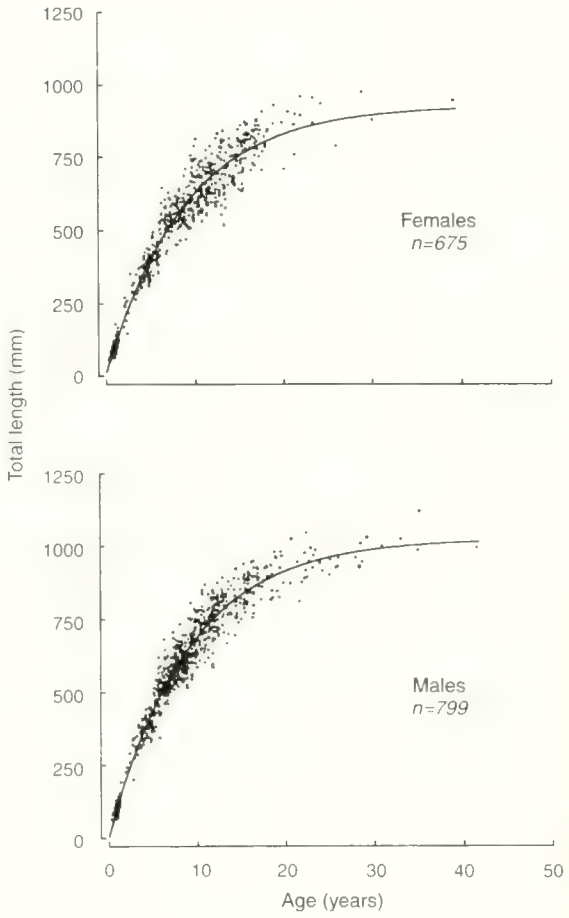

Figure 4

Von Bertalanffy growth curves fitted to length-at-age data for females and males of *Glaucosoma hebraicum* caught on the lower west coast of Australia. n = number of fish used to construct growth curves.

Trends exhibited by reproductive variables

The macroscopic characteristics of the different stages in gonadal development, and of the cytological characteristics of the ovaries at different stages based on an examination of histological sections, are given in Table 1.

Because stages I (virgin) and II (immature) in the development of both the ovaries and testes of *G. hebraicum* were difficult to separate macroscopically, data for these two stages were pooled in the case of both sexes. Furthermore, it is also important to recognize that spawning stage (VI) ovaries are distinguished from prespawning stage (V) ovaries almost exclusively on the basis of their possession of hydrated oocytes or postovulatory follicles (or both) when histological sections were employed to examine the ovary at a finer scale. However, because *G. hebraicum* is a multiple spawner, i.e. produces eggs in batches at intervals, any "prespawning" stage ovary may already have produced some hydrated oocytes, but been at an intermediate phase in which the next batch of yolk granule oocytes had not yet become hydrated. The prevalence of females with prespawning ovaries that had already spawned on one or more occasions would be expected to increase during the spawning period. Likewise, the main difference between prespawning and spawning testes, i.e. the ability of the testes to produce milt when subjected to physical pressure, may often represent different phases in the cyclical changes undergone in the testis during the spawning period. For the above reasons, the data on stage-V and stage-VI ovaries and testes were pooled for describing the change in compositions of the gonadal maturity stages of each sex during the year.

Between May 1996 and April 1998, the mean monthly GSIs for females of *G. hebraicum* that were greater than the L_{50} of 301 mm at first maturity were always low in winter (June to August) and early spring (September), i.e. <1.0 but then rose sharply to reach a peak of ca. 2.8 in mid-summer (January), before declining markedly during early to mid-autumn (March and April) (Fig. 5). The trends displayed by the mean monthly GSIs for males of *G. hebraicum*, that were greater than the $L_{50}$of 320 mm at first maturity, paralleled those just described for females.

Because the trends exhibited by the mean monthly GSIs for females and males were the same during both 12 month periods, the percentage contributions of the different gonadal stages of the females and males of *G. hebraicum*, that were longer than the L_{50}, were pooled for each of the corresponding calendar months. The gonads of female *G. hebraicum* in July were at stages I–II, i.e. virgin or immature (Fig. 6). Fish with ovaries at stage III (developing) were first found in August, albeit only a few fish, and those at stage IV

Table 1

Characteristics of the macroscopic stages in the development of the gonads of *Glaucosoma hebraicum* and, in the case of the ovaries, the histological characteristics of each corresponding ovarian stage. Terminology for oocyte stages follows Khoo (1979).

Stage	Macroscopic appearance	Histological characteristics
I–II (virgin and immature)	Gonads very small. Ovaries transparent and oocytes not visible. Testes strandlike and gray-white.	Ovigerous lamellae highly organized. Oogonia and chromatin nucleolar oocytes and, in more advanced ovaries, early perinucleolar oocytes are present. These oocyte stages are present in all subsequent ovarian stages.
III (developing)	Gonads slightly larger than at stage I or II. Ovaries pinkish, blood capillaries visible in ovary walls. Testes white and more lobular.	Early and late perinucleolar oocytes and yolk vesicle oocytes present.
IV (maturing)	Gonads markedly larger. Ovaries reddish-orange, capillaries more conspicuous and some yolk granule oocytes visible through ovary wall. Milt is not extruded when pressure is applied to testes.	Yolk vesicle and yolk granule oocytes abundant.
V (prespawning)	Ovaries orange and occupy most of space in body cavity. Extensive capillaries in ovary walls. Milt appears when testes placed under firm pressure.	Yolk granule oocytes abundant and in tight groups.
VI (spawning)	Same as for stage V, but with hydrated oocytes visible through ovarian wall and only slight pressure required to release milt from testes.	Hydrated oocytes or postovulatory follicles (or both) present.
VII (spent)	Gonads smaller than at stages V or VI. Ovaries flaccid. Some yolk granule oocytes still visible through ovary wall. Testes pinkish-red.	Remnant yolk granule oocytes present, typically undergoing atresia.
VIII (recovering spent)	Gonads greatly reduced in size and dark red. Testes strandlike.	Lamellae not organized as in early stages of development and contain extensive scar tissue. Any remaining yolk granule oocytes are atretic.

(maturing) and stages V and VI (prespawning and spawning) were first recorded in September and October, respectively. Stage-V and stage-VI ovaries collectively became the most prevalent group in females in November and formed the most dominant group by far in December to March. The samples in February and March contained a few female fish with stage I–II ovaries, but none with ovaries at either stage III or IV (Fig. 6). These trends provide overwhelming circumstantial evidence that any female whose ovaries have developed to at least stage III by November will progress through to maturity during the following months of the spawning period. Thus, the L_{50} for females at first maturity was calculated by using the percentage of ovaries with stages III and IV, as well as those with stages V–VIII. Although females with stage-VII (spent) and stage-VIII (recovering spent) ovaries were found between January and May, the majority of ovaries were at stages I–II in the latter month and all were at stages I–II in June. The trends exhibited by the pattern of gonadal development in males were essentially the same as those just described for females and thus the L_{50} of males was likewise calculated with the percentage of testes at stages III–VIII (Fig. 7).

The following account of the trends exhibited by the oocyte composition of ovaries is based on an histological examination of the ovaries of large fish well above the L_{50} at first maturity. The oocytes in ovaries in July and August were almost exclusively at the chromatin nucleolar stage. Ovaries with yolk vesicles first appeared in September, and those with yolk granules were first found in October. Yolk granule oocytes became increasingly prevalent in ovaries in November and dominated the complement of their larger oocytes between December and March. Some of the residual yolk granule oocytes in April and all of those in May were undergoing atresia. No yolk vesicle or yolk granule oocytes were found in June. Hydrated oocytes were first found in ovaries in November and were present in many ovaries between December and March and in a few ovaries in April, but were found neither in May nor in the immediately ensuing months. Small numbers of postovulatory follicles were present in about a third of the ovaries of large females caught between December and March. The oocyte diameters of individual large *G. hebraicum* caught in each month of the spawning period produced a series of modes (data not shown).

Length and age at maturity

The sex of *Glaucosoma hebraicum* was not able to be determined by macroscopic examination of the gonads until it had reached ca. 150 mm in length. During the main part of the spawning period, i.e. December to March, the gonads of all female and male *G. hebraicum* <250 mm were at the earliest stages of development, i.e. I–II (Fig. 7). Gonads at stages III–VIII were first found in the 250–299 mm length class of females and in the 300–349 mm length class of males. The presence of such gonads demonstrated that the fish were maturing or that spawning was occurring or had been completed (see earlier). The prevalence of ovaries at stages III–VIII increased to ca. 80% in the 300–349 mm length class and to 100% in all females >450 mm. The gonads of all males >450 mm were at stages III–VIII (Fig. 7). The L_{50}'s for the lengths of female and male *G. hebraicum* at first maturity, derived from the logistic curve fitted to the percentage contributions of fish with gonads at stages III–VIII in sequential 50-mm length classes, were 301 and 320 mm, respectively (Fig. 7).

Individual *G. hebraicum* could first be sexed macroscopically during their second year of life. Although relatively few two-, three- and four-year-old fish were caught, the trends exhibited by the proportion of gonads at stages III–VIII in both sexes during the spawning period were consistent. One female and no males at two years of age possessed gonads at stage III or greater (Fig. 8). However, 50% of three-year-old female and male fish, and all five-year-old females and all six-year-old males possessed such gonads and were thus regarded as mature. The A_{50}'s for the age at first maturity of females and males were 3.4 and 3.3 years, respectively.

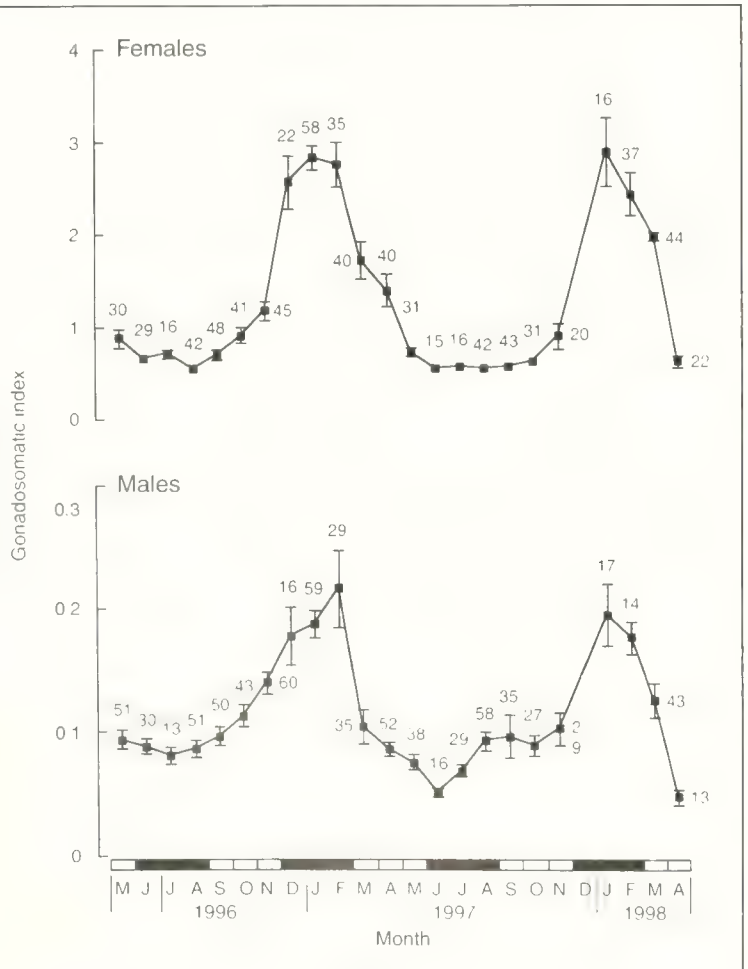

Figure 5

Mean monthly gonadosomatic indices ±1SE for females and males of *Glaucosoma hebraicum* caught in offshore waters between May 1996 and April 1998. Data in this Figure and Figure 6 are restricted to females and males ≥L_{50} at first maturity. Numbers of fish used to calculate each mean GSI are shown.

Mortality

Using the regression equation developed by Ralston (1987), in combination with the estimated value for the von Bertalanffy growth coefficient, k = 0.111/year, we estimated the instantaneous coefficient of natural mortality, M, to be 0.25/year. The catch curve analysis of the combined age composition data, for the 620 dhufish older than 9 years and longer than the MLL (Fig. 9), produced an estimate of the instantaneous coefficient of total mortality, Z, of 0.21/year (95% confidence interval: 0.19 to 0.23/year). The estimate of Z remained at about this level as the initial age was increased to 15 years and then declined to ca. 0.15/year at 24 to 27 years (Fig. 9). It subsequently became less precise as the initial age increased. An estimate of Z of 0.10/year was obtained when the observed maximum age of 41 years was substituted into Hoenig's (1983) regression equation. However, when the sample size of 620 fish was taken into account, with the expression for the expected maximum age (Hoenig 1983, Appendix A), Z was estimated to be 0.22/year.

Discussion

Ontogenetic changes in habitat of *Glaucosoma hebraicum*

Extensive sampling for *G. hebraicum* during the present study, allied with data obtained with an echo sounder and video footage, demonstrate that this species changes habitat as it increases in size. Thus, *G. hebraicum* <150 mm was found to live in areas near reefs where the substrate is firm and sponges often occur (Bergquist and Skinner, 1982). The reduction in the numbers of 1+ dhufish caught by trawling in this type of habitat in late autumn, when their lengths were about 130 mm, probably reflects a movement by the members of this

cohort, as they increase in size, from a habitat that could be trawled to one where reefs occur and where it was not possible to trawl. This conclusion is supported by the fact that the few dhufish of 150–300 mm that were caught were collected from low-lying reefs, i.e. reefs that contained rock ledges up to 30 cm in height. In contrast, *G. hebraicum* >300 mm typically occupy areas where there are substantial limestone and coral reef formations and their large size would make them less susceptible to predation in a habitat where large predatory species, such as the Samson fish (*Seriola hippos*) and the pink snapper (*Pagrus auratus*) are found (Hesp, personal obs.).

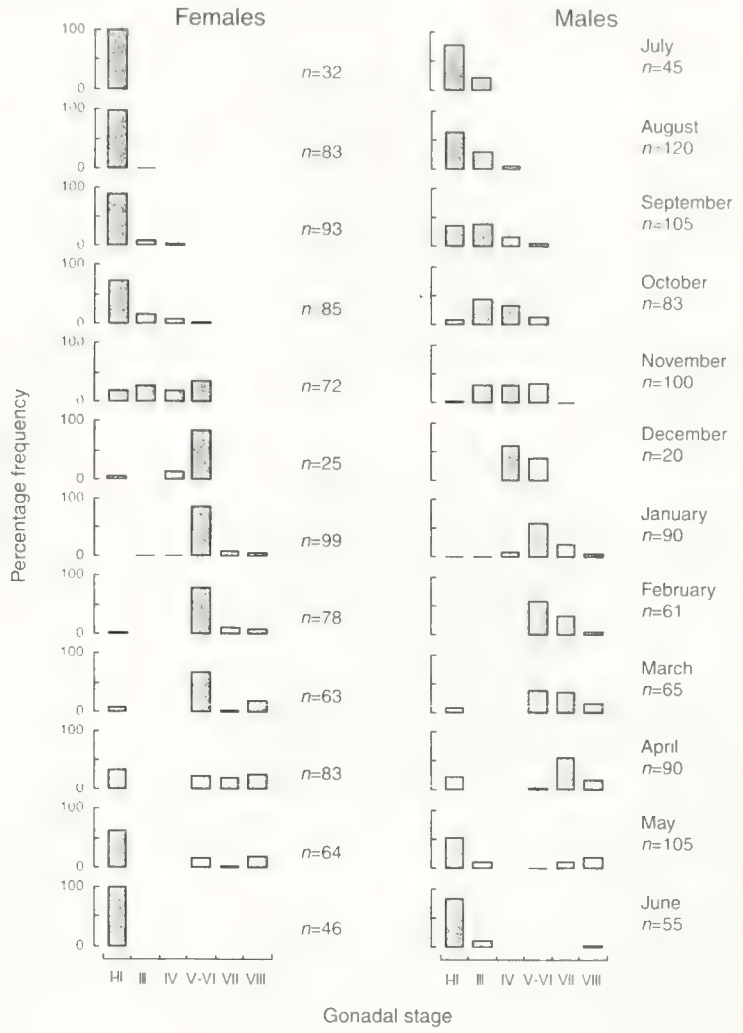

Figure 6

Percentage frequency histograms for gonadal maturity stages of females and males of *Glaucosoma hebraicum*. Data have been pooled for corresponding months in the period May 1996 to April 1998. Sample sizes (n) are given for each month.

Aging

The trends exhibited by the marginal increments on sectioned otoliths of *G. hebraicum* show that an opaque zone is formed annually in the otoliths of this species. However, comparisons between the number of opaque zones on individual otoliths prior to and after sectioning demonstrate that, after this species has reached six years in age, one or more of these zones often become visible only after the otolith has been sectioned. This demonstrates that earlier estimates of the age of older *G. hebraicum*, which were based on the number of opaque zones visible in whole otoliths (Sudemeyer et al.[1]), were almost certainly often too low.

An inability to detect all of the opaque zones in the whole otoliths of older fish is largely attributable to the fact that, as the otolith increases in width, it becomes increasingly difficult to distinguish between the zones at the periphery of the otolith. This problem parallels the situation recorded for several other medium-size to large teleosts, such as Pacific hake (*Merluccius productus*) (Beamish, 1979), starry flounder (*Platyichthys stellatus*) (Campana, 1984) and blue-spotted flathead (*Platycephalus speculator*) (Hyndes et al., 1992). Our results demonstrate that, although most *G. hebraicum* are less than 25 years old, some females and males live for longer than 30 years and very occasionally for up to about 40 years.

Other species that are typically caught by commercial and recreational rod and hand-line fishermen when fishing for dhufish include pink snapper (*Pagrus auratus*), Sampson fish (*Seriola hippos*), silver trevally (*Pseudocaranx dentex*), breaksea cod (*Epinephelides armatus*), and occasionally also King George whiting (*Sillaginodes punctata*). The maximum total lengths and weights recorded for these five species are 1300 mm and 19.5 kg for pink snapper, 1753 mm and 53.6 kg for Samson fish, 938 mm and 10.0 kg for silver trevally, 550 mm and 2.9 kg for breaksea cod, and 690 mm and 4.8 kg for King George whiting, compared with 1219 mm and 25.8 kg for dhufish (Hutchins and Thompson 1995).

Although reliable data have been obtained for the age and growth of a number of commercial and recreational fish species that live in nearshore coastal or estuarine waters in southwestern Australia (e.g. Chubb et al., 1981; Hyndes et al., 1992, 1996; Hyndes and Potter, 1996, 1997; Laurenson et al., 1994; Fairclough et al., 2000; Sarre and Potter, 2000), comparable data for those species that are found in and around reefs in deeper waters in southwestern Australia are restricted to those recorded for *G. hebraicum* in this paper and for the King George whiting *Sillaginodes*

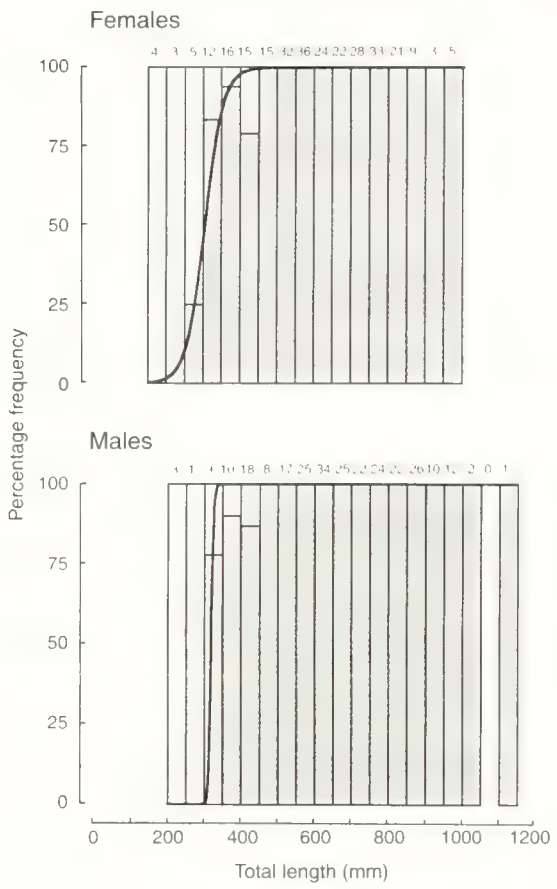

Figure 7

Percentage frequency of occurrence of gonads at stages I–II (□) and stages III–VIII (■) in each sequential 50-mm class of female and male *Glaucosoma hebraicum* caught between December and March. The logistic curve has been fitted to the data for fish with gonads at stages III–VIII. The sample size is given for each length class.

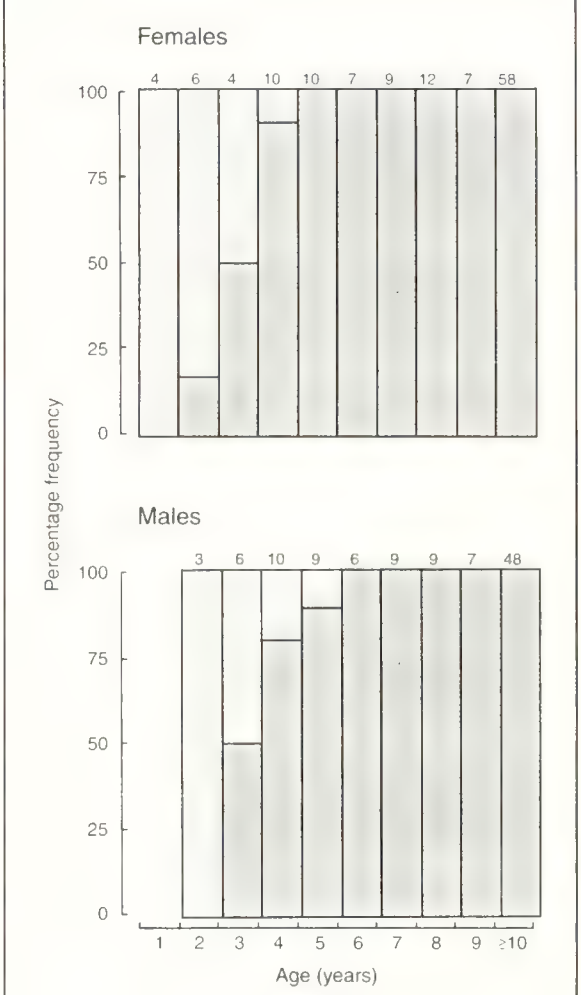

Figure 8

Percentage frequency of occurrence of gonads at stages I–II (□) and stages III–VIII (■) in each sequential age class of female and male *Glaucosoma hebraicum* caught between December and March. The sample size is given for each age class.

punctata by Hyndes et al. (1998). Using data from the lower west coast of Australia, Hyndes et al. (1998) estimated the von Bertalanffy growth parameters, L_∞, k, and t_0, for King George whiting to be 538 mm TL, 0.47/year, and 0.13 years, respectively, for females, and 500 mm TL, 0.53/year and 0.16 years, respectively, for males. Although there are no published studies on the growth of pink snapper and silver trevally in Western Australia, the growth of these two species has been investigated in New Zealand by Francis et al. (1992) and by James (1984) respectively. The parameters L_∞, k, and t_0 were estimated to be 720 mm FL (fork length), 0.106/year and –0.75 years, respectively, for pink snapper, and ranged from 436 to 448 mm FL, from 0.27 to 0.43/year and from –1.6 to –0.6 years, respectively, for silver trevally. Although the growth coefficient, k, for dhufish, i.e. 0.111/year, was similar to that for pink snapper, it was appreciably less that that for both King George whiting and silver trevally. Dhufish had an asymptotic length ca. 35% greater than that of pink snapper and approximately twice those of King George whiting and silver trevally.

The lengths of females at maturity have been reported as ca. 350 mm FL for silver trevally (James, 1984) and 413 mm TL for King George whiting (Hyndes et al., 1998) and have been estimated as 237 mm FL for pink snapper (calculated from Crossland, 1977). Although maturity is first achieved by the females of snapper and dhufish at 30% of their respective asymptotic lengths, it is attained by the females of King George whiting and silver trevally at 75–80% of their asymptotic lengths. This finding implies that the last two species have a higher reproductive load *sensu* Cushing (1981). Thus, although these four species reach maturity and begin to occupy promi-

nent reefs at similar lengths, the growth of silver trevally and King George whiting slows after maturation, whereas that of snapper and dhufish continues appreciably after they have reached maturity.

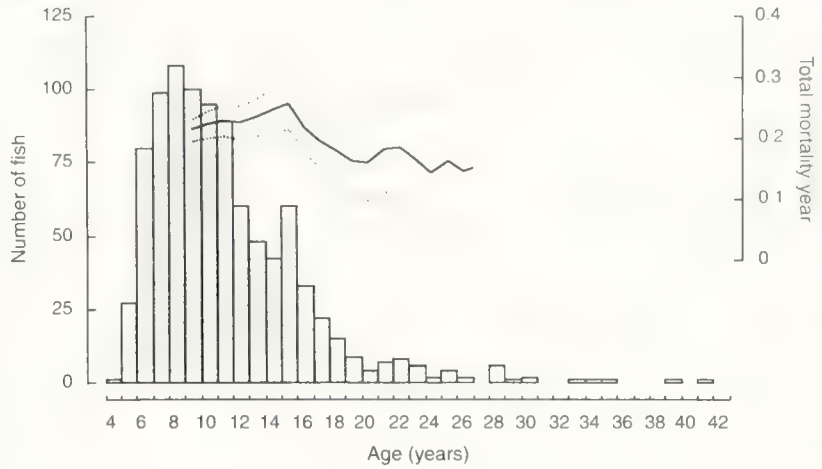

Figure 9

Age composition of *Glaucosoma hebraicum*, that were caught at lengths ≥ the minimum legal length of 500 mm, and maximum likelihood estimates (±95% confidence limits) for the instantaneous coefficients of total mortality/year, Z, determined from subsets of these data selected by using different initial ages.

Spawning location, period, and mode

Glaucosoma hebraicum with gonads at stages VI (spawning) and VII (spent) were caught in waters ranging from 10 to 150 m in depth and at distances of 3 to 50 km from the shore and between latitudes 28°55′ and 32°45′S. Thus, the spawning of dhufish is not apparently restricted to any particular water depth or region along the coast. However, because *G. hebraicum* greater than 300–320 mm in length (their size at first maturity) were almost invariably caught only around limestone or coral reef formations, this species apparently spawns in the vicinity of reefs.

Because hydrated eggs and postovulatory follicles were found in at least some of the ovaries of large females in each month between November and April, it is evident that *G. hebraicum* spawn between the end of spring and middle of autumn. Although some fish commenced spawning in November, the mean GSI of female fish in that month was still well below its maximum. This indication that only a small amount of spawning occurs in November is consistent with the fact that many of the ovaries of large fish were still at stages III and IV. Although most of the ovaries of large females caught in May 1997 contained some vitellogenic oocytes, these oocytes were usually undergoing atresia and the ovaries of other large fish in that month were either spent or resting. Furthermore, none of the ovaries of large *G. hebraicum* caught in May contained hydrated oocytes. This finding provides strong evidence that the spawning period does not extend into May. There is also strong evidence that spawning peaks in January and February. For example, by January, the ovaries and testes of most large fish were at stages V or VI, i.e. prespawning or spawning, and, for the first time, some were spent or even recovering spent (stages VII and VIII). The maintenance of the GSIs of females at their maxima in both January and February is attributable to the fact that, because *G. hebraicum* is a multiple spawner, new batches of hydrated oocytes were continually being developed in the ovary during these two months. However, the GSIs of females and males both declined precipitously in March, which demonstrates that, in the case of ovaries, the release of eggs during spawning was not being compensated for by a comparable production of new batches of mature eggs. As spawning activity peaked in January and February, it was appropriate to use 1 February as the birth date of *G. hebraicum* when assigning an age to each fish.

The fact that, during the spawning season, mature ovaries of *G. hebraicum* often contained yolk vesicle, yolk granule, and hydrated oocytes and, in some cases, also postovulatory follicles, implies that this species is a multiple spawner *sensu* deVlaming (1983), i.e. individual females release eggs on more than one occasion in a spawning season. The oocytes of individual female *G. hebraicum* during the spawning period ranged widely in size and, in many cases, their diameters formed relatively discrete modes in oocyte diameter-frequency distributions. The ovaries of *G. hebraicum* thus contain batches of oocytes that are presumably released at different times. Multiple-batch spawning over a protracted period enables a greater total number of eggs to be produced and released during a spawning period and results in eggs becoming discharged at different times (McEvoy and McEvoy, 1992), which would increase the overall chance of recruitment success.

Implications of the biology of *Glaucosoma hebraicum* for fisheries management

The age composition data for dhufish older than 9 years and larger than the MLL reflect an average level of the instantaneous coefficient of total mortality, Z, of 0.21/year. This value is consistent with the estimate obtained from the observed maximum age, taking into account the sample size of 620 fish (Hoenig, 1983). The much lower value obtained for Z, with Hoenig's (1983) regression equation for fish, i.e. 0.10/year, does not take into account sample size.

The estimate of the instantaneous coefficient of natural mortality, M, of 0.25/year, that was calculated with Ralston's (1987) equation, exceeds the average value of 0.21/year for the instantaneous coefficient of total mortality, which was estimated from the catch curve. Examination of the residuals from the regression line fitted by Ralston (Fig. 8.1 in

Ralston, 1987) suggests that the precision of this estimate of the instantaneous coefficient of natural mortality is likely to be relatively low. It was therefore concluded that the value for M derived from Ralston's equation represented an overestimate. A more detailed examination of the catch curve data suggested, but was unable to demonstrate conclusively, that the level of total mortality experienced by the older fish when they were young was less than that which is now being experienced by the population. Indeed, if the decline in the estimated value for Z, displayed in Fig. 9, was extrapolated to an age of 40 years, the total mortality exhibited by the oldest age classes (when, as young fish, they first became fully vulnerable to the fishery) would be ca. 0.1/year. Such a value, which might be only slightly greater than the natural mortality, matches the estimate of Z calculated from the observed maximum age with Hoenig's (1983) regression equation. However, such agreement may be fortuitous because the latter estimate should represent the total mortality experienced by the fish within the sample, i.e. from age 9, rather than just the mortality of the older fish. Nevertheless, if the level of natural mortality, M, is ca. 0.1/year and the average level of instantaneous coefficient of total mortality, Z, from age 9 years is ca. 0.21/year, the current level of fishing mortality, F, would exceed 0.11/year.

In the nearshore waters along the lower west coast of Australia where this species is most heavily fished, the abundance of *G. hebraicum* has declined to a level that is of concern to fishermen. Numerous anecdotal reports indicate that commercial and dedicated recreational fishermen, such as those who provided the samples for this study, now tend to move further offshore in order to obtain catches of *G. hebraicum* comparable with those they used to obtain in waters closer to the coast. However, many recreational fishermen still continue to fish for *G. hebraicum* (and other species) in the traditional areas where dhufish were fished in the past. The expansion of the fishery for dhufish to include waters farther offshore, allied with the increasing use of global positioning systems (GPSs) to improve fishing efficiency, is increasing the level of exploitation of the stock as a whole.

The fact that there are indications that the fishing-induced mortality of dhufish may now exceed natural mortality and that ongoing expansion in the extent to which fishermen are moving offshore (and also, in the case of recreational fishermen, in a northwards and southwards direction from the main metropolitan region of Perth) will further increase fishing pressure, is of concern to the managers responsible for the fishery for *G. hebraicum*. However, because our sampling regime was not designed specifically at determining the levels of fishing mortality to which *G. hebraicum* is being subjected, there is clearly a need to undertake a study in which the main aim is to achieve this objective. If such research were to confirm our preliminary findings that fishing mortality is reaching an unacceptable level, there will be an urgent need to use the biological data produced during the current study to refine the management plans designed to conserve this species.

Female and male *G. hebraicum* first reach sexual maturity at the end of their third year of life when they are just over 300 mm in length and they reach 500 mm, the MLL for capture, when they are about 7 and 6 years old, respectively. Thus, on average, the female and male dhufish that live until they reach the MLL will have had the opportunity to have spawned for four and three years, respectively, before they can legally be retained following capture. Ongoing research at the state fisheries laboratory in Western Australia has indicated that ca. 50% of fish caught in waters of 20–30 m depth die on being released back into the water and that this percentage increases to ca. 95% for fish brought to the surface from depths greater than 40 m (Moran[2]). Thus, the use of a MLL is likely to be of only limited value for conserving this species as fishing effort continues to increase. It is therefore important to introduce measures that will conserve *G. hebraicum* by maintaining the catches of this species at a level consistent with the requirements for ecological sustainability. Examples of such management controls might include closing areas to commercial and recreational fishing (particularly those around reefs that are especially heavily fished) introducing quotas for commercial fish catches, making adjustments to the number of commercial licenses, further restricting the bag limit for recreational fishermen, and limiting the number of recreational fishermen that can fish in a given area. Furthermore, because the Fremantle Maritime Centre has successfully cultured *G. hebraicum* (Cleary et al.[3]), there is also now the potential for restocking this species in areas in which it has become severely depleted.

Acknowledgments

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Longitudinal logbook survey designs for estimating recreational fishery catch, with application to ayu (*Plecoglossus altivelis*)

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Abstract—Longitudinal surveys of anglers or boat owners are widely used in recreational fishery management to estimate total catch over a fishing season. Survey designs with repeated measures of the same random sample over time are effective if the goal is to show statistically significant differences among point estimates for successive time intervals. However, estimators for total catch over the season that are based on longitudinal sampling will be less precise than stratified estimators based on successive independent samples. Conventional stratified variance estimators would be negatively biased if applied to such data because the samples for different time strata are not independent. We formulated new general estimators for catch rate, total catch, and respective variances that sum across time strata but also account for correlation stratum samples. A case study of the Japanese recreational fishery for ayu (*Plecoglossus altivelis*) showed that the conventional stratified variance estimate of total catch was about 10% of the variance estimated by our new method. Combining the catch data for each angler or boat owners throughout the season reduced the variance of the total catch estimate by about 75%. For successive independent surveys based on random independent samples, catch, and variance estimators derived from combined data would be the same as conventional stratified estimators when sample allocation is proportional to strata size. We are the first to report annual catch estimates for ayu in a Japanese river by formulating modified estimators for day-permit anglers.

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Angler surveys are widely used in fishery management to estimate recreational catch, and there is an extensive body of literature on this subject (see Guthrie et al., 1991). Pollock et al. (1994) published a manual on angler survey methods and their applications in fishery management. The first purpose of our study is to make two very important points for the designers of recreational fishery surveys: 1) longitudinal surveys taking repeated measures on the same random sample of anglers or boats over time are better than successive independent surveys if the goal is to determine significant trends in catch and fishing effort, and 2) stratified surveys, or successive independent surveys based on random independent samples of anglers or boats, are better than longitudinal surveys if the goal is to obtain precise estimates of annual total catch and fishing effort. If longitudinal fisheries data sets are used to estimate annual catches, then correlations between monthly sample observations must be taken into account when evaluating the precision of catch estimates. This problem is not addressed in the literature, and the variance estimation procedures for this situation are unclear. The second purpose of our study is to estimate the annual catch of ayu (*Plecoglossus altivelis*) in a river because no estimates have been reported in Japan.

In our study, we formulated a new method for accurate variance estimation with longitudinal fishery data, exemplified by a case study of the recreational fishery for ayu in Nakagawa River in Tochigi Prefecture, Japan (Fig. 1). Annual catch estimates based on sums of monthly estimates were compared with those based on combined data for each angler or boat throughout the fishing season. We demonstrate how use of a design with repeated measures facilitates determination of significant seasonal trends in catches, and show the usefulness of combined (nonstratified) data analysis. We also estimate the total annual catch of the ayu fishery by formulating modified estimators for day-permit anglers (anglers who are granted permits to take fish for one day).

Materials and methods

Case study of ayu

We used longitudinal data collected for the Japanese ayu fishery to compare estimators of effort and catch and their associated variance estimators. Ayu is the most popular target species of recreational anglers in rivers in Japan. In the Nakagawa River (Fig. 1), the upstream run of wild juvenile ayu from the coast begins in late March to early April, and is completed by early July. Ayu mature and spawn from September to November, and then die after spawning. Cooperatives release both hatchery-produced and wild juveniles caught

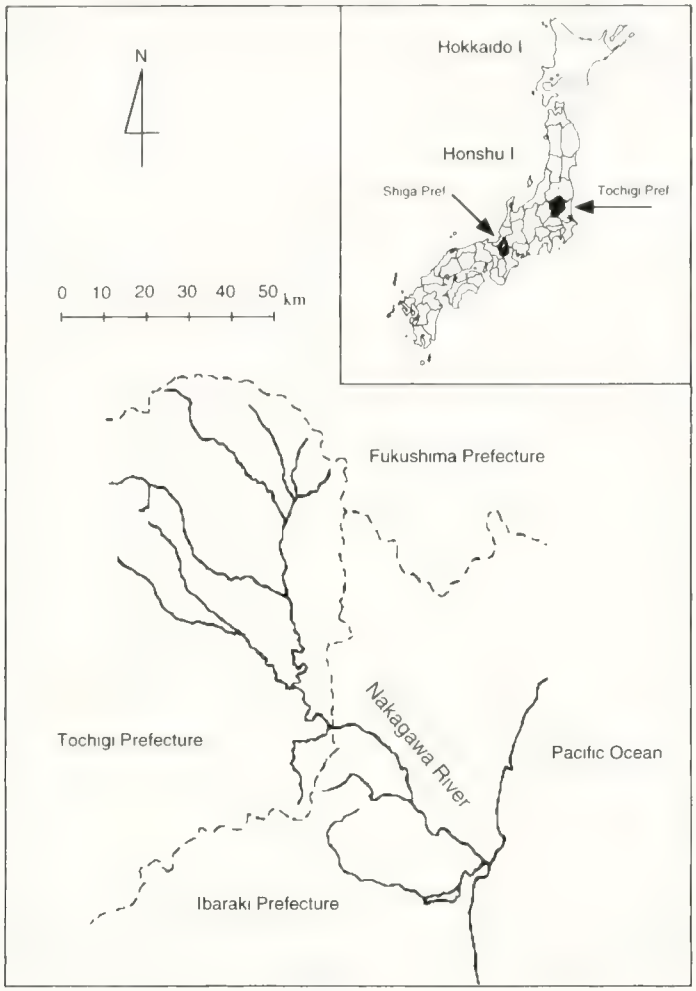

Figure 1

Location of the angler survey. Bold lines in the lower figure indicate the area of the Nakagawa River where the survey was conducted.

in Biwako Lake, Shiga Prefecture (Fig. 1) from early April to the end of May. Thus, recreational anglers catch both naturally recruited wild juveniles and transplanted wild juveniles from Biwako Lake and hatchery-produced ayu released by the cooperatives. Both hatchery and wild stocks consist of a single year class that recruits in the spring. The river fishing season for ayu begins on June 1st and closes at the end of October. To estimate the annual ayu catch by recreational anglers in the Nakagawa River, we conducted a longitudinal log book survey in 1993.

Sampling procedure

There are four cooperatives that set fishing rights on the Nakagawa River in Tochigi Prefecture. Fishing permits for ayu are sold at the cooperatives and fishing tackle shops, and these permits are valid over the entire Nakagawa River in the prefecture. The cooperatives record the total number of season- and day-permits sold, and a complete list of season-permit anglers is available. An *a priori* sample size of 120 anglers (an expected sampling fraction of about 0.5% of the total number of season-permit anglers) was allocated to the four cooperatives in proportion to the number of season-permits sold (Table 1). Anglers who possess a permit (season or day) can fish for ayu over the whole Nakagawa area, regardless of where the permit was purchased. Hence, we treated the samples as if they were drawn from the population by simple random sampling, even though they were drawn by stratified random sampling of cooperatives.

We asked the cooperatives to select samples randomly, but the samples were drawn arbitrarily. The selection, however, was not a purposive sampling; therefore we treated them as random samples. The sampled season-permit anglers were asked to record catch data throughout the fishing season, including each fishing date, the number of ayu caught, and the fishing site, on a printed form, which was returned after the fishing season was over. To estimate the total catch in weight, we also surveyed the body weights of ayu in recreational catches by month. The

Table 1

The number of permits sold in 1993, sample size, and the number of logbooks returned by the four fishermen's cooperative associations along the Nakagawa River. n = number of anglers sampled.

Fishermen's cooperative associations	Number of season permits sold	Number of day permits	n	Number of logbooks returned
Hokubu	11,314	6520	70	64
Nanbu	6391	1946	30	21
Chuo	1911	231	10	10
Motegi	2346	369	10	9
Total	21,962	9066	120	104

primary sampling unit in a population of season-permit anglers or boat owners (i.e. party-boat owners or personal-boat owners) was an angler or a boat owner, and the secondary sampling unit was a fishing day. We selected anglers or boat owners by simple random sampling without replacement from a list of anglers or boat owners, and asked a sample of anglers or boat owners to record catch data on all fishing days throughout the survey. Because all the secondary sampling units were surveyed, we regarded this as a single-stage cluster sampling procedure (Cochran, 1977).

Estimation of total catch by month

Estimation for season-permit anglers or boat owners The principal notations for estimation of the total catch for season-permit anglers or party-boat owners are as follows (Cochran, 1977; Pollock et al., 1994):

N = total number of sampling units (season-permit angler or party-boat or personal-boat owner; known number);
n = sample size drawn from the population N;
M_k = total number of fishing days in the population in kth month (to be estimated);
M_{ik} = total number of fishing days in kth month of selected ith sample;
$\overline{M}_k$ = mean number of fishing days per sampling unit in kth month (to be estimated);
C_{ik} = number of fish caught by ith sample in kth month;
R_k = catch rate of kth month (to be estimated);
$C_k^{(s)}$ = total catch by season-permit anglers or by party-boat owners or personal-boat owners in kth month (to be estimated).

The catch rate is the number of fish caught per sampling unit each day. For logbook surveys, the ratio of the mean is the preferable estimator of catch rate (Jones et al.,1995; Pollock et al., 1997).

The ratio and the variance for the catch rate is estimated by

$$\hat{R}_k = \frac{\sum_{i=1}^{n} C_{ik}}{\sum_{i=1}^{n} M_{ik}}, \qquad (1)$$

$$\hat{V}(\hat{R}_k) = \frac{N}{M_k^2}\frac{N-n}{n(n-1)}\sum_{i=1}^{n}(C_{ik} - M_{ik}\hat{R}_k)^2. \qquad (2)$$

This variance estimator is obtained by dividing Equation 6.9 in Cochran (1977, p. 155) by the total number of fishing days in the kth month M_k. In Equation 2, M_k is unknown; hence we approximated the variance estimate by using the estimator of M_k as follows (Thompson, 1992, p. 62):

$$\hat{V}(\hat{R}_k) = \frac{N-n}{N\bar{M}_k^2 n(n-1)}\sum_{i=1}^{n}(C_{ik} - M_{ik}\hat{R}_k)^2, \qquad (3)$$

where $\hat{M}_k = N\bar{M}_k$. The variance of $\hat{M}_k$ is estimated by $\hat{V}(\hat{M}_k) = N^2\hat{V}(\bar{M}_k)$, where $\bar{M}_k$ is the mean number of fishing days per sampling unit in kth month. The estimator and the variance are as follows (Cochran, 1977, p. 249, from Eq. 9A.2):

$$\bar{M}_k = \frac{1}{n}\sum_{i=1}^{n} M_{ik}, \qquad (4)$$

$$\hat{V}(\bar{M}_k) = \frac{N-n}{Nn(n-1)}\sum_{i=1}^{n}(M_{ik} - \bar{M}_k)^2. \qquad (5)$$

The total number of fish caught in kth month is estimated by

$$\hat{C}_k = \hat{M}_k\hat{R}_k = N\bar{M}_k\hat{R}_k = N\frac{\sum_{i=1}^{n} M_{ik}}{n}\frac{\sum_{i=1}^{n} C_{ik}}{\sum_{i=1}^{n} M_{ik}} = \frac{N}{n}\sum_{i=1}^{n} C_{ik}. \qquad (6)$$

This results in an unbiased estimator. When the total number of fishing days M_k is unknown, the ratio estimator coincides with the unbiased estimator. The variance is evaluated by (Cochran, 1977, p. 249, from Eq. 9A.2):

$$\hat{V}(\hat{C}_k^{(s)}) = \frac{N(N-n)}{n(n-1)} \sum_{i=1}^{n} (C_{ik} - \hat{C}_k)^2 \qquad (7)$$

where $\hat{C}_k = \sum_{i=1}^{n} C_{ik}/n$.

Estimation for day-permit anglers We estimated the catch of day-permit anglers separately. The notations for day-permit anglers catch estimation are as follows:

D = total number of day-permits sold through the season (known);
D_k = total number of day-permits sold in k th month (known);
d_k = total number of day-permit anglers who returned logbooks in kth month;
$R_k^{(d)}$ = catch rate of kth month for day-permit anglers;
$C_k^{(d)}$ = total catch by day-permit anglers in kth month (to be estimated).

The estimator of total number of fish caught by day-permit anglers in kth month is

$$\hat{C}_k^{(d)} = D_k \hat{R}_k^{(d)}. \qquad (8)$$

where the catch rate for day-permit anglers, estimated by the sample mean, is

$$\hat{R}_k^{(d)} = \frac{1}{d_k} \sum_{i=1}^{d_k} c_{ik}. \qquad (9)$$

The variance estimator of $\hat{C}_k^{(d)}$ is (Cochran, 1977, p. 26, from Eq. 2.20):

$$\hat{V}(\hat{C}_k^{(d)}) = D_k^2 \hat{V}(\hat{R}_k^{(d)}) = \frac{D_k(D_k - d_k)}{d_k(d_k-1)} \sum_{i=1}^{d_k} (C_{ik} - \hat{R}_k^{(d)})^2. \qquad (10)$$

Total monthly catch of season- and day-permit anglers The total catch by season- and day-permit anglers in kth month is C_k, which is estimated by

$$\hat{C}_k = \hat{C}_k^{(s)} + \hat{C}_k^{(d)}. \qquad (11)$$

These two total estimates are obtained from independent samples (season- and day-permit anglers); therefore the variance is estimated by adding the variances:

$$\hat{V}(\hat{C}_k) = \hat{V}(\hat{C}_k^{(s)}) + \hat{V}(\hat{C}_k^{(d)}). \qquad (12)$$

The total catches in weight in kth month are estimated by using the mean body weight of the species in kth month ($\bar{w}_k$) estimated from the survey of individual body weights by

$$\hat{W}_k = \hat{W}_k^{(s)} + \hat{W}_k^{(d)} = \hat{C}_k \hat{\bar{w}}_k, \qquad (13)$$

where $\hat{W}_k^{(s)}$ and $\hat{W}_k^{(d)}$ are the total catches in weight for season- and day-permit anglers, given by $\hat{W}_k^{(s)} = \hat{C}_k^{(s)} \hat{\bar{w}}_k$ and $\hat{W}_k^{(d)} = \hat{C}_k^{(d)} \hat{\bar{w}}_k$. In general, season-permit and day-permit anglers fish in the same location; therefore we assumed the same mean body weight for both kinds of anglers. The samples for estimating C_k and $\bar{w}_k$ are independent; therefore the variances are estimated by using Goodman's (1960) formula:

$$\hat{V}(\hat{W}_k) = \hat{V}(\hat{W}_k^{(s)}) + \hat{V}(\hat{W}_k^{(d)}) \qquad (14)$$

where $\hat{V}(\hat{W}_k^{(s)}) = \hat{\bar{w}}_k^2 \hat{V}(\hat{C}_k^{(s)}) + \hat{C}_k^{(s)2} \hat{V}(\hat{\bar{w}}_k) + \hat{V}(\hat{C}_k^{(s)}) \hat{V}(\hat{\bar{w}}_k)$

and $\hat{V}(\hat{W}_k^{(d)}) = \hat{\bar{w}}_k^2 \hat{V}(\hat{C}_k^{(d)}) + \hat{C}_k^{(d)2} \hat{V}(\hat{\bar{w}}_k) + \hat{V}(\hat{C}_k^{(d)}) \hat{V}(\hat{\bar{w}}_k)$.

The mean body weight of fish in kth month is estimated from a survey of individual body weights (w_{ik} of l_k fish caught on the fishing grounds). The estimator for kth month and its variance estimator are

$$\hat{\bar{w}}_k = \sum_{i=1}^{l_k} w_{ik}/l_k$$

and $$\hat{V}(\hat{\bar{w}}_k) = \sum_{i=1}^{l_k} (w_{ik} - \hat{\bar{w}}_k)^2 / \{l_k(l_k-1)\}.$$

The total fishing days in kth month is estimated as the sum of the fishing days estimates of the season-permit anglers and the day-permit anglers by

$$\hat{M}_{Tk} = \hat{M}_k + D_k \qquad (15)$$

and the variance is estimated by $\hat{V}(\hat{M}_{Tk}) = N^2 \hat{V}(\hat{\bar{M}}_k)$ because D_k is known.

Estimation of annual catch

Method 1 (based on monthly estimates) The annual catch is estimated by summing monthly catch estimates over the entire fishing season (K months). The point estimator is

$$\hat{C} = \sum_{k=1}^{K} \hat{C}_k = \sum_{k=1}^{K} \hat{C}_k^{(s)} + \sum_{k=1}^{K} \hat{C}_k^{(d)} = \hat{C}^{(s)} + \hat{C}^{(d)}. \qquad (16)$$

When the same sample of anglers reports catches throughout the season, the sampling is not independent in each month, and monthly catch estimates are auto-correlated. Taking this correlation into account, the variance estimator is

$$\begin{aligned} \hat{V}(\hat{C}) &= \hat{V}(\hat{C}^{(s)}) + \hat{V}(\hat{C}^{(d)}) \\ &= \sum_{k=1}^{K} \hat{V}(\hat{C}_k^{(s)}) + 2 \sum_{k<k'}^{K} \widehat{\mathrm{Cov}}(\hat{C}_k^{(s)}, \hat{C}_{k'}^{(s)}) \\ &+ \sum_{k=1}^{K} \hat{V}(\hat{C}_k^{(d)}) + 2 \sum_{k<k'}^{K} \widehat{\mathrm{Cov}}(\hat{C}_k^{(d)}, \hat{C}_{k'}^{(d)}). \end{aligned} \qquad (17)$$

The covariance between two total estimates of season-permit anglers is estimated by (see Appendix 1, from Cochran, 1977, p. 25)

$$\widehat{\mathrm{Cov}}(\hat{C}_k^{(s)}, \hat{C}_{k'}^{(s)}) = \frac{N(N-n)}{n(n-1)} \sum_{i=1}^{n} (C_{ik} - \hat{\bar{C}}_k)(C_{ik'} - \hat{\bar{C}}_{k'}). \quad (18)$$

The fourth term of Equation 17 is equal to 0 if a different sample of day-permit anglers is drawn in each month.

The total catch in weight is estimated by

$$\hat{W} = \sum_{k=1}^{K} \hat{W}_k = \sum_{k=1}^{K} \hat{W}_k^{(s)} + \sum_{k=1}^{K} \hat{W}_k^{(d)} = \hat{W}^{(s)} + \hat{W}^{(d)} \quad (19)$$

and the variance estimator is similar to Equation 17 but has a slightly different covariance which is

$$\widehat{\mathrm{Cov}}(\hat{W}_k^{(s)}, \hat{W}_{k'}^{(s)}) = \hat{\bar{w}}_k \hat{\bar{w}}_{k'} \widehat{\mathrm{Cov}}(\hat{C}_k^{(s)}, \hat{C}_{k'}^{(s)}). \quad (20)$$

This covariance estimator was derived by the delta method (Seber, 1982, p. 7, see Appendix 2), which coincides with a covariance when $\hat{\bar{w}}_k$ and $\hat{\bar{w}}_{k'}$ are constant.

The mean annual catch rate is estimated for season-permit anglers or boats by

$$\hat{R}^{(s)} = \frac{\hat{C}^{(s)}}{\hat{M}^{(s)}}, \quad (21)$$

where $\hat{M}^{(s)} = \sum_{k=1}^{K} \hat{M}_k = N \sum_{k=1}^{K} \hat{\bar{M}}_k$.

Here $\hat{\bar{M}}_k$ is given by Equation 4. The total effort is estimated by $\hat{M}^{(s)} + D$. The approximate variance of $\hat{V}(\hat{R}^{(s)})$ is given by the delta method (Seber, 1982, p. 7; Appendix 3), that is

$$\hat{V}(\hat{R}^{(s)}) = \frac{1}{\hat{M}^{(s)2}} \left\{ \begin{array}{l} \hat{V}(\hat{C}^{(s)}) + \left(\frac{\hat{C}^{(s)}}{\hat{M}^{(s)}} \right)^2 \hat{V}(\hat{M}^{(s)}) \\ -2 \frac{\hat{C}^{(s)}}{\hat{M}^{(s)}} \widehat{\mathrm{Cov}}(\hat{C}^{(s)}, \hat{M}^{(s)}) \end{array} \right\}, \quad (22)$$

where $\hat{V}(\hat{C}^{(s)})$ is given by Equation 17, and the variance of the total number of fishing days is estimated by

$$\hat{V}(\hat{M}^{(s)}) = N^2 \left\{ \sum_{k=1}^{K} \hat{V}(\hat{\bar{M}}_k) + 2 \sum_{k<k'}^{K} \widehat{\mathrm{Cov}}(\hat{\bar{M}}_k, \hat{\bar{M}}_{k'}) \right\}. \quad (23)$$

Here $\hat{V}(\hat{\bar{M}}_k)$ is given by Equation 5 and the covariance of two sample means is estimated by (Cochran, 1977, p. 25)

$$\widehat{\mathrm{Cov}}(\hat{\bar{M}}_k, \hat{\bar{M}}_{k'}) = \frac{N-n}{Nn(n-1)} \sum_{i=1}^{n} (M_{ik} - \hat{\bar{M}}_k)(M_{ik'} - \hat{\bar{M}}_{k'}). \quad (24)$$

The estimator of covariance between $\hat{C}^{(s)}$ and $\hat{M}^{(s)}$ is similar to Equation 18 (see Appendix 1):

$$\widehat{\mathrm{Cov}}(\hat{C}^{(s)}, \hat{M}^{(s)}) = \frac{N(N-n)}{n(n-1)} \sum_{i=1}^{n} (C_i - \hat{\bar{C}})(M_i - \hat{\bar{M}}), \quad (25)$$

where C_i and M_i are the number of fish caught and the number of fishing days of ith season-permit angler or boat owner throughout the season, respectively, and

$$\hat{\bar{C}}_k = \sum_{i=1}^{n} C_{ik} / n,$$

and

$$\hat{\bar{M}} = \sum_{i=1}^{n} M_i / n.$$

The mean number of fishing days per sampling unit (season-permit angler or boat) is estimated by

$$\hat{\bar{M}} = \frac{\hat{M}^{(s)}}{N}$$

and the variance estimator is

$$\hat{V}(\hat{\bar{M}}) = \frac{1}{N^2} \hat{V}(\hat{M}^{(s)}),$$

where $\hat{M}^{(s)}$ and $\hat{V}(\hat{M}^{(s)})$ are already derived from Equation 21 and Equation 23, respectively.

The catch rate of day-permit anglers over the season is estimated by

$$\hat{R}^{(d)} = \frac{\hat{C}^{(d)}}{D}$$

and the variance is

$$\hat{V}(\hat{R}^{(d)}) = \frac{1}{D^2} \hat{V}(\hat{C}^{(d)}),$$

where $\hat{C}^{(d)}$ and $\hat{V}(\hat{C}^{(d)})$ are given in Equation 8 and Equation 10, respectively.

Method 2 (based on total annual catch of each angler or boat owner) Another procedure for estimating annual catch is to use annual data rather than monthly catch for individual anglers or boats. The advantages of this procedure are that covariances between months do not have to be considered and estimators are much less complicated than those obtained using method 1. Equations derived for monthly estimation can be used without modification for this procedure.

Modified estimators for day-permit anglers

We could not conduct a survey of day-permit anglers, so we substituted $\hat{R}_k$ for $\hat{R}_k^{(d)}$ in Equation 8. In addition, the total number of day permits sold in kth month (D_k) was

unknown. Hence, we slightly modified the procedure for estimating D_k by $D\hat{p}_k$, where p_k is the proportion of day permits sold in kth month to the annual total number of day permits sold (D).

Day permits issued by the cooperatives are sold mainly in fishing tackle shops. We selected four tackle shops and surveyed the total number of day permits sold at the selected jth fishing tackle shop (D_j), and the total number of day permits sold at the selected jth fishing tackle shop in kth month (D_{jk}). The proportion of day permits sold in kth month was estimated by

$$\hat{p}_k = \frac{\sum_{j=1}^{h} D_{jk}}{\sum_{j=1}^{h} D_j},$$

where h is the number of fishing tackle shops selected from a total of H shops. The evaluation of the variance of $\hat{p}_k$ was similar to Equation 3:

$$\hat{V}(\hat{p}_k) = \frac{H(H-h)}{D^2 h(h-1)} \sum_{j=1}^{h} (D_{jk} - D_j \hat{p}_k)^2.$$

Some day permits, however, were sold at the fishing sites, and the above variance estimator was not appropriate for this situation. Assuming $\Sigma_{j=1}^{h} D_j$ was selected by simple random sampling from D, we evaluated the variance by (Cochran, 1977, p. 52, Eq. 3.8)

$$\hat{V}(\hat{p}_k) = \frac{D - \sum_{j=1}^{h} D_j}{D\left(\sum_{j=1}^{h} D_j - 1\right)} \hat{p}_k(1-\hat{p}_k).$$

The modified estimator for the total number of fish caught by day-permit anglers in kth month is

$$\hat{C}_k^{(d)} = D\hat{p}_k\hat{R}_k. \tag{26}$$

Here $\hat{p}_k$ and $\hat{R}_k$ are independent because these are estimated from different survey data. The variance of revised $\hat{C}_k^{(d)}$ was estimated by using Goodman's (1960) method:

$$\hat{V}(\hat{C}_k^{(d)}) = D^2\left\{\hat{R}_k^2\hat{V}(\hat{p}_k) + \hat{p}_k^2\hat{V}(\hat{R}_k) + \hat{V}(\hat{p}_k)\hat{V}(\hat{R}_k)\right\}.$$

The total fishing days in kth month was estimated by Equation 15 but in this case D_k was unknown. The modified estimator was

$$\hat{M}_{Tk} = \hat{M}_k + D\hat{p}_k$$

and the variance was slightly revised as

$$\hat{V}(\hat{M}_{Tk}) = N^2\hat{V}(\bar{\hat{M}}_k) + D^2\hat{V}(\hat{p}_k).$$

The annual catch was estimated by Equation 16, substituting Equation 8 by Equation 26. In this case, we estimated $\hat{C}_k^{(d)}$ and $\hat{C}_{k'}^{(d)}$ from the same sample of season-permit anglers. Hence, the fourth term of the covariance in Equation 17 must be considered. The approximate covariance is estimated by (see Appendix 4)

$$\widehat{\mathrm{Cov}}(\hat{C}_k^{(d)}, \hat{C}_{k'}^{(d)}) = D^2\hat{p}_k\hat{p}_{k'}\widehat{\mathrm{Cov}}(\hat{R}_k, \hat{R}_{k'}), \tag{27}$$

where the covariance between $\hat{R}_k$ and $\hat{R}_{k'}$ is

$$\widehat{\mathrm{Cov}}(\hat{R}_k, \hat{R}_{k'}) = \frac{1}{N^4}\begin{pmatrix} \frac{1}{\bar{\hat{M}}_k\bar{\hat{M}}_{k'}}\widehat{\mathrm{Cov}}(\hat{C}_k^{(s)}, \hat{C}_{k'}^{(s)}) \\ -\frac{\hat{C}_{k'}^{(s)}}{\bar{\hat{M}}_k\bar{\hat{M}}_{k'}^2}\widehat{\mathrm{Cov}}(\hat{C}_k^{(s)}, \bar{\hat{M}}_{k'}) \\ -\frac{\hat{C}_k^{(s)}}{\bar{\hat{M}}_k^2\bar{\hat{M}}_{k'}}\widehat{\mathrm{Cov}}(\bar{\hat{M}}_k, \hat{C}_{k'}^{(s)}) \\ +\frac{\hat{C}_k^{(s)}\hat{C}_{k'}^{(s)}}{\bar{\hat{M}}_k^2\bar{\hat{M}}_{k'}^2}\widehat{\mathrm{Cov}}(\bar{\hat{M}}_k, \bar{\hat{M}}_{k'}) \end{pmatrix}.$$

Here $\widehat{\mathrm{Cov}}(\hat{C}_k^{(s)}, \hat{C}_{k'}^{(s)})$ and $\widehat{\mathrm{Cov}}(\bar{\hat{M}}_k, \bar{\hat{M}}_{k'})$ are already given by Equation 18 and Equation 24. The other covariance components are

$$\widehat{\mathrm{Cov}}(\hat{C}_k^{(s)}, \bar{\hat{M}}_{k'}) = \frac{N-n}{n^2(n-1)}\sum_{i=1}^{n}(C_{ik} - \bar{\hat{C}}_k)(M_{ik'} - \bar{\hat{M}}_{k'})$$

$$\widehat{\mathrm{Cov}}(\bar{\hat{M}}_k, \hat{C}_{k'}^{(s)}) = \frac{N-n}{n^2(n-1)}\sum_{i=1}^{n}(C_{ik'} - \bar{\hat{C}}_{k'})(M_{ik} - \bar{\hat{M}}_k).$$

The annual catch in weight was estimated by Equation 19, substituting Equation 8 with Equation 26. The covariance in the fourth term of $\hat{V}(\hat{W})$ in Equation 17 was estimated with Equation 20 by

$$\widehat{\mathrm{Cov}}(\hat{W}_k^{(d)}, \hat{W}_{k'}^{(d)}) = \bar{\hat{w}}_k\bar{\hat{w}}_{k'}\widehat{\mathrm{Cov}}(\hat{C}_k^{(d)}, \hat{C}_{k'}^{(d)})$$

where $\widehat{\mathrm{Cov}}(\hat{C}_k^{(d)}, \hat{C}_{k'}^{(d)})$ is given in Equation 27.

Results

In 1993, 21,962 season permits and 9066 day permits were sold (Table 1). The total number of day permits sold at the four fishing tackle shops was 4776, and the number (proportion, $\hat{p}_k$) sold was 2732 (0.572) in June, 1,189 (0.249) in July, 716 (0.150) in August, 124 (0.026) in September, and 15 (0.003) in October.

We received 104 logbooks from the 120 season-permit anglers sampled, a return rate of 86.7%. In addition, two anglers voluntarily submitted logbooks, but we did not include these unsolicited returns because they were not randomly selected. The modes of the catch rates by the sampled anglers were from five to ten fish per month (Fig. 2). The histograms show a large variation in the catch rate among season-permit anglers. The peak fishing season was from June to July. In September, the number of anglers decreased, and the fishing season ended in October. The

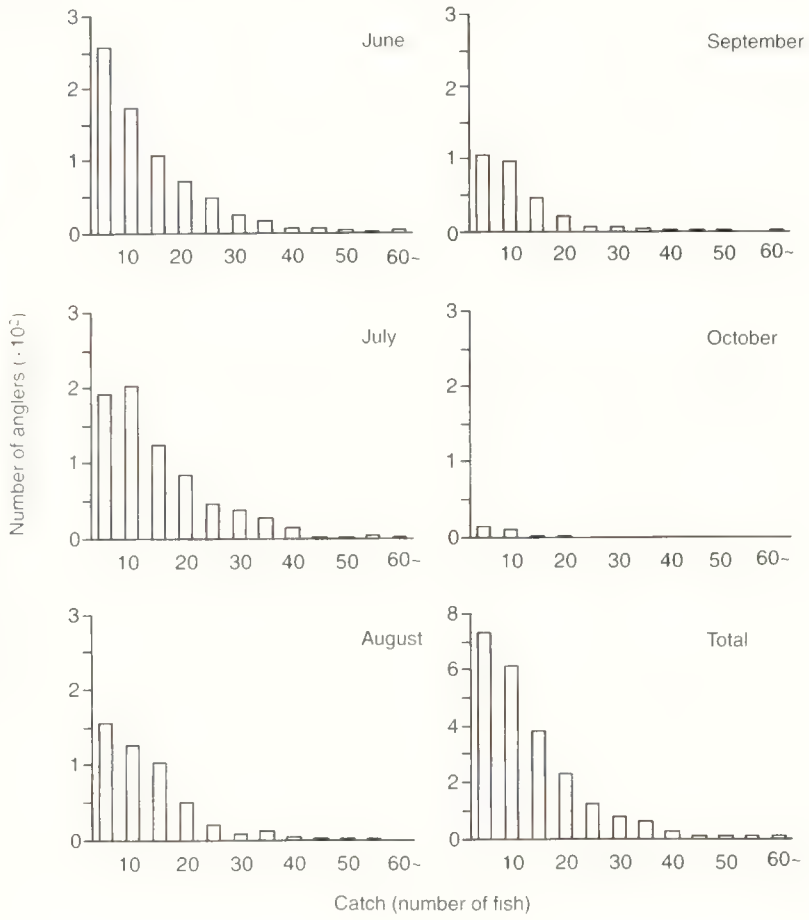

Figure 2

Distributions of the catch rate of ayu by month for 104 sampled season-permit anglers in the Nakagawa River.

modes of the number of fishing days per season-permit angler were five for all months. The variation in the number of fishing days among anglers was also large (Fig. 3).

Monthly plots of the total number of fish caught versus the number of fishing days showed linear relationships (Fig. 4). The variation in Figure 4 indicates differences in the skill of the anglers. The monthly number of anglers decreased over the fishing season. Figure 5 shows the monthly changes in the total number of fishing days, the total number of fish caught, and the catch rate for the 104 sampled anglers. The decline in number of fish caught was largely due to the decrease in fishing days. The change in catch rate indicated a decline in the abundance of the stock.

The mean body weight of ayu was greatest in June (Fig. 6) and was affected by a method of fishing for ayu called "Tomo-zuri" angling, which takes advantage of the attacking behavior of ayu when another fish enters its territory. Anglers attach a "call" fish (a live ayu) above a treble hook that snares the territorial wild fish, as it attacks the "call" fish. Because larger individuals establish territories earlier than smaller ayu, fish caught in June were predominantly the larger individuals.

Reflecting the monthly trend in the number of fishing days, 89% of the total annual catches of season-permit anglers and 98% of those of day-permit anglers were taken from June to August (Table 2). The catch by day-permit anglers was substantially smaller than anticipated, estimated at about 2% of season-permit anglers' catch in both numbers and total weight. CVs ranged from 7% to 12% in June and July for all parameters; however, they were higher in August and September, ranging from 10% to 20%. In October, CVs exceeded 43% for total catch in number and weight. The decreasing precision of the monthly catch rate estimates was caused by the decrease in anglers (n_k) (Figs. 4 and 5).

The CVs of annual estimates of $\overline{M}$ and $\hat{M}_T$ by method 1 were about 7%, but that of $\hat{R}^{(s)}$ was about 20% (Table 2) because we evaluated the covariance terms for the number of catches and fishing days between months; those were

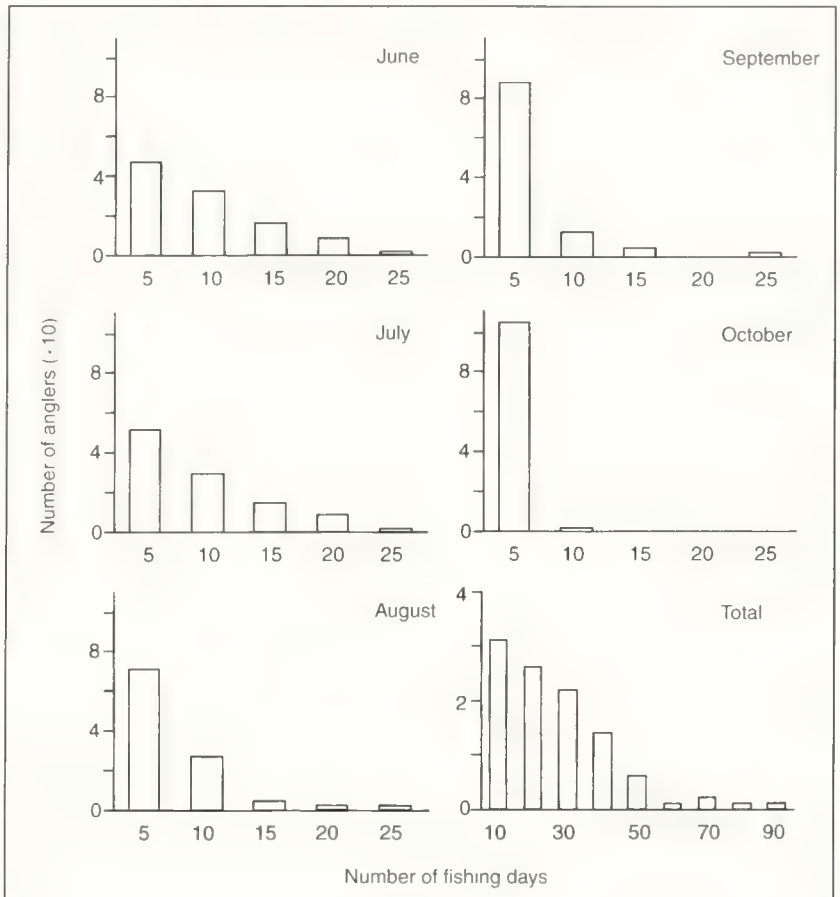

Figure 3

Distributions of the ayu fishing days per angler by month for 104 sampled season-permit anglers in the Nakagawa River.

$\widehat{\mathrm{Cov}}(\hat{C}_k^{(s)}, \hat{C}_{k'}^{(s)})$ in $\hat{V}(\hat{C}^{(s)})$ and $\widehat{\mathrm{Cov}}(\bar{M}_k, \bar{M}_{k'})$ in Equation 22. The CVs of $\hat{C}$ and $\hat{W}$ were also evaluated at about 21% and were strongly affected by the covariances between months in Equation 17. The variance of the total number estimate $\hat{V}(\hat{C})$ was 1.2604×10^{12}, and variance by neglecting the covariance term in Equation 17 was 1.2230×10^{11}. The CV of $\hat{C}$ without the covariance term was 6.53%. If we neglect the covariance, the variance is substantially underestimated. The variance was 10.31 times larger when the covariance term was included.

We obtained similar point estimates of annual catch by method 2 (Total$^{\text{meth. 2}}$ in Table 2). The CVs of $\bar{M}$, M_T, $\hat{C}$, and $\hat{W}$ for day-permit anglers were about 7%, but that of $\hat{R}^{(s)}$ was reduced from 19.7% to 6.6% by not considering the covariance terms. The CVs of $\hat{C}$ and $\hat{W}$ dropped about 10% from 21% without the covariance. Similar point estimates and smaller variance estimates were obtained. The variance estimate of the annual catch obtained by method 1 with covariances (1.2604×10^{12}) was 4.11 times larger than that by method 2 (3.0667×10^{11}).

The relationship between the sample size and the precision of the annual catch estimate for season-permit anglers was examined. We calculated the values $\hat{V}(\hat{C})$ for various values of n by using Equation 7. To obtain precision over the season for CVs of $\hat{C}^{(s)}(=\sqrt{\hat{V}(\hat{C})}/\hat{C})$ below 10%, a sample size of 120 or more is required (Table 3).

A high positive correlation in catches between adjacent months was detected (Table 4). We mapped anglers (objects) and fishing days (categories) into a two-dimensional graph by correspondence analysis (Hayashi, 1950; Benzécri, 1992) using the function "pq3.prcomp" in S version 4 (Chambers and Hastie, 1992). Correspondence analysis showed the relations between rows and columns in a frequency table graphically as points in a common low-dimensional space (Clausen, 1998). Both objects (rows) and categories (columns) of variables are represented as points in such a way that an object is relatively close to its category and relatively far from other categories (Leeuw and van Rijckevorsel 1988). For example, the 72nd angler fished 10 days in June, five days in July, seven days in August, three days in September, one day in October, and this angler was mapped closed to June, reflecting the month of his highest fishing effort (Fig. 7). The results suggest several fishing patterns with high catch seasons in June–July, July–

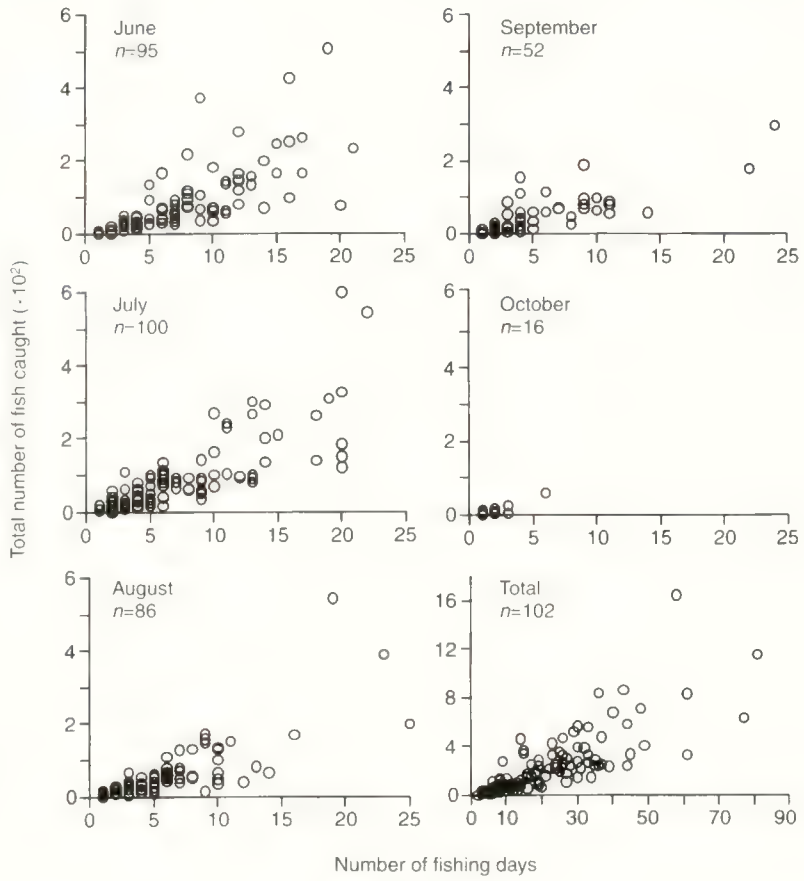

Figure 4

Relationship between the number of fishing days and the number of fish caught by 104 sampled season-permit anglers in the Nakagawa River.

August, August–September, and September–October, resulting high correlations between adjoining months, and large covariances between distant months (Table 4).

The prime advantage of a longitudinal study is its effectiveness for studying change, and a repeated measures analysis of variance can be applied to a complete data set with a constant correlation (Diggle et al., 1994). However, our data set was incomplete because the number of anglers who fish in each month changed (see n in Fig. 4) and had a different correlation structure among month (Table 4). We tested the differences between successive monthly catch estimates of season-permit anglers by using a parametric bootstrapping method. In the central limit theorem, the sample distribution of a monthly total catch estimate can be regarded as a normal with the mean $C_k^{(s)}$ and the variance $\hat{V}(C_k^{(s)})$. Based on the two point estimates, variance estimates and the correlation coefficient between successive two months, we generated 10,000 bivariate normal random variables (Gentle, 1998). The means and 95% confidence intervals of the differences between two monthly total catch estimates were –226,561 [–650,404~203,080] for June and July, 870,720 [455,091~1,277,402] for July and August, 470,594 [161,013~783,168] for August and September, and 537,488 [290,905~782,727] for September and October. Significance levels were corrected for multiple testing by using the Bonferroni ajustment factor (Sokal and Rohlf, 1995).The confidence interval for June and July straddled 0, showing no significant difference. On the other hand, three other confidence intervals did not include 0; therefore the monthly differences were statistically significant (Fig. 8).

Discussion

Bias and source of variation

The estimate of the total annual catch of ayu by the recreational fishery was the first obtained in Japan and was much larger than expected. The total number of day-permits sold was 9066, and was quite small (1.9%) compared with the estimated total number of anglers (477,520).

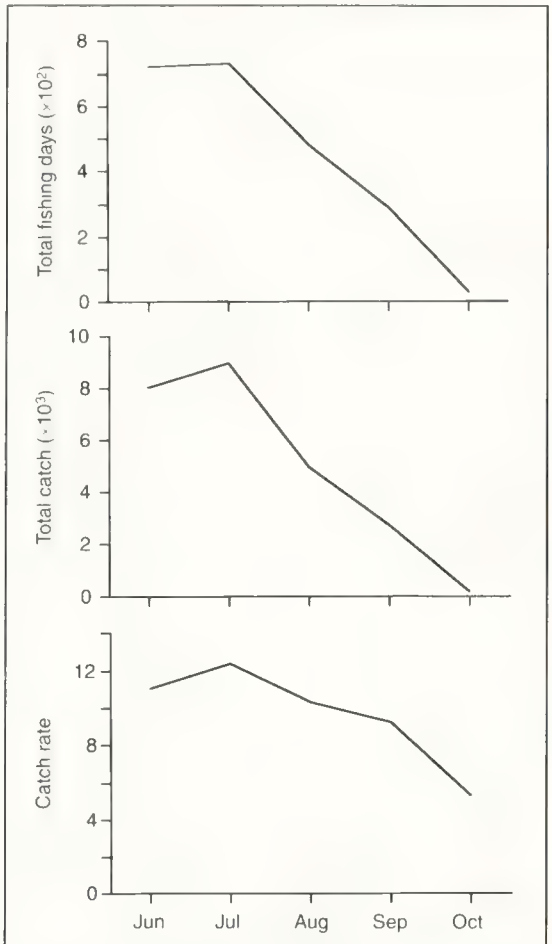

Figure 5

Monthly changes in the number of fishing days, total catch, and catch rate for 104 sampled anglers in the Nakagawa River.

Although the difference in the catch rate between day- and season-permit anglers was unknown, the influence of this bias on the total catch estimates would be minor. In order to check the bias, however, one could conduct a logbook survey of day-permit anglers. Sixteen anglers of the total sample (13%) in our study did not return logbooks and therefore may have caused a bias in our estimates; however no attempt was made to evaluate the difference between nonrespondents and respondents. The angler sample was drawn arbitrarily by the cooperatives but was not a random sample in the strictest sense. If cooperative anglers tended to be selected, this could have been a source of bias.

The source of variation in total catch is the variation in the catch of the sampling unit, including differences in fishing days, skill of the anglers, and the number of anglers that a party boat could accommodate. A stratified sampling scheme based on categories of anglers or boats is effective for this situation. The weakest point in the use of logbook surveys, perhaps, is that the catch data are reported by those who catch the fish and by boat owners with monetary interests. To what extent the anglers might have exaggerated or under-reported their catch is not known. Party boat owners may record lower than actual catches to reduce taxes. To examine this possible source of bias, on-site surveys should be conducted. For the ayu fishery in the Nakagawa River, an access point survey may be practical (Pollock et al., 1994). When comparatively complete lists of boat owners and anglers are available, logbook surveys based on these lists, combined with on-site surveys, are appropriate.

Longitudinal and stratified survey designs

Longitudinal surveys taking repeated measures on the same random sample over time are better than successive independent surveys if the designer's goal is to show statistically significant differences in the estimates between time intervals. Monthly estimates showing seasonal trends

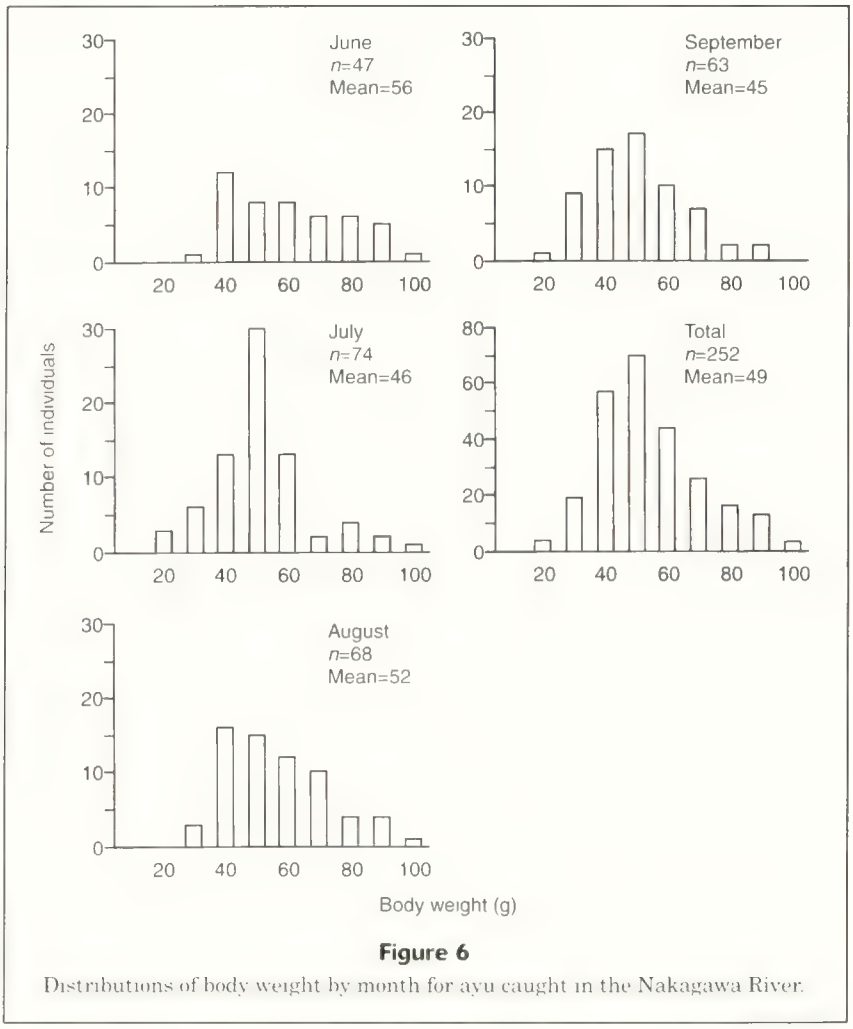

Figure 6

Distributions of body weight by month for ayu caught in the Nakagawa River.

can be obtained by the equations derived in our study. In such repeated measure designs, the most precise estimates of annual catch are obtained by method 2. On the other hand, stratified surveys, or successive independent surveys between time intervals based on random samples of anglers or boats, are better than longitudinal surveys if the designer's goal is to obtain precise estimates of total effort, or catch (or total effort and catch), over the entire season. Stratification by month would improve the precision of annual estimates even more if estimates varied greatly across months. Stratified sampling allows independent monthly estimates, and monthly estimates can be summed to produce precise estimates over time. In the absence of correlations between monthly sample observations, the estimated variance of annual estimates can be obtained simply by adding the estimated variances of the monthly estimates. The estimated variances of annual estimates stratified by month would be considerably less than those of annual estimates based on repeated monthly observations of a one-time annual sample.

If method 2 is used to analyze data obtained by such independent surveys, how would the precision of the estimator compare with the precision of a stratified estimator? For simplicity, we consider a population that is divided into two subpopulations of N_1, N_2 units, respectively. The stratified estimator of the population total and the respective variance are

$$\hat{Y} = N_1\bar{y}_1 + N_2\bar{y}_2,$$
$$\hat{V}(\hat{Y}) = N_1^2\hat{V}(\bar{y}_1) + N_2^2\hat{V}(\bar{y}_2),$$

where $\bar{y}_1$ and $\bar{y}_2$ are the sample means for sample sizes of n_1 and n_2. On the other hand, those obtained by method 2 are

$$\hat{Y}_r = \frac{N_1 + N_2}{n_1 + n_2}(n_1\bar{y}_1 + n_2\bar{y}_2),$$
$$\hat{V}(\hat{Y}_r) = \left\{\frac{n_1(N_1 + N_2)}{n_1 + n_2}\right\}^2\hat{V}(\bar{y}_1) + \left\{\frac{n_2(N_1 + N_2)}{n_1 + n_2}\right\}^2\hat{V}(\bar{y}_2).$$

Subtracting Y_r from Y, we have

Table 2

Estimated parameters and coefficients of variation (in parentheses). Total$^{meth.\ 1}$ = total estimated by summing monthly estimates (method 1). Total$^{meth.\ 2}$ = total estimated by combining data throughout the season (method 2). $R^{(s)}$ = catch rate for season-permit anglers. M = mean number of fishing days per season-permit anglers. M_T = total number of fishing days (season+day-permit anglers). $C^{(s)}$ = total catch in number for season-permit anglers. $C^{(d)}$ = total catch in number for day-permit anglers. C = total catch in number (season+day-permit anglers). $W^{(s)}$ = total catch in weight for season-permit anglers. $W^{(d)}$ = total catch in weight for day-permit anglers. W = total catch in weight (season+day-permit anglers).

Parameter	June	July	August	September	October	Total$^{meth.\ 1}$	Total$^{meth.\ 2}$
$R^{(s)}$	11.12	12.37	10.29	9.29	5.35	11.04	11.04
	(0.087)	(0.075)	(0.115)	(0.187)	(1.495)	(0.197)	(0.066)
M	6.92	7.05	4.62	2.80	0.28	21.66	21.65
	(0.073)	(0.075)	(0.101)	(0.153)	(0.291)	(0.073)	(0.073)
M_T	157,231	157,047	102,722	61,687	6,152	484,839	484,628
	(0.071)	(0.074)	(0.100)	(0.152)	(0.290)	(0.072)	(0.071)
$C^{(s)}$	1,690,440	1,914,495	1,042,772	570,800	32,732	5,251,241	5,251,241
	(0.116)	(0.115)	(0.154)	(0.179)	(0.437)	(0.214)	(0.105)
$C^{(d)}$	57,658	27,915	13,982	2,186	152	101,894	100,108
	(0.087)	(0.077)	(0.118)	(0.197)	(1.528)	(0.056)	(0.066)
C	1,748,099	1,942,410	1,056,755	572,987	32,884	5,353,135	5,351,349
	(0.112)	(0.114)	(0.152)	(0.178)	(0.435)	(0.210)	(0.103)
$W^{(s)}$ (t)	94.64	88.30	53.26	25.85	1.48	263.53	253.90
	(0.125)	(0.122)	(0.159)	(0.184)	(0.439)	(0.213)	(0.107)
$W^{(d)}$ (t)	3.23	1.29	0.71	0.10	0.01	5.34	4.84
	(0.099)	(0.086)	(0.124)	(0.202)	(1.530)	(0.065)	(0.069)
W (t)	97.86	89.59	53.98	25.95	1.49	268.86	258.74
	(0.122)	(0.120)	(0.157)	(0.183)	(0.437)	(0.209)	(0.105)

Table 3

Coefficient of variations of the total catch estimate $C^{(s)}$ (method 2) for various sample sizes (number of anglers).

n	CV	n	CV	n	CV
10	0.3401	110	0.1025	230	0.0709
20	0.2405	120	0.0982	250	0.0680
30	0.1963	130	0.0943	300	0.0621
40	0.1700	140	0.0909	400	0.0538
50	0.1521	150	0.0878	500	0.0481
60	0.1388	160	0.0850	600	0.0439
70	0.1285	170	0.0824	700	0.0406
80	0.1202	180	0.0802	800	0.0380
90	0.1134	190	0.0780	900	0.0358
100	0.1075	200	0.0760	1000	0.0340

Table 4

Estimated variance-covariance matrix ($\cdot 10^{10}$) for the monthly estimates of catch (number) by season-permit anglers in number by Equation 17 (lower diagonal) and the correlation coefficient $r(C_{ik}, C_{i'k})$ (upper diagonal, in bold font). The diagonal component refers to $\hat{V}(\hat{C}_k)$ and the lower half refers to $\widehat{\mathrm{Cov}}(C_k^{(s)}, C_{k'}^{(s)})$.

Month	Jun	Jul	Aug	Sep	Oct
Jun	3.837	**0.67**	**0.43**	**0.30**	**–0.03**
Jul	6.011	4.862	**0.65**	**0.49**	**0.08**
Aug	9.422	4.434	2.578	**0.65**	**0.28**
Sep	10.681	6.258	1.456	1.038	**0.44**
Oct	10.725	6.336	1.522	0.069	0.020

$$\hat{Y} - \hat{Y}_c = \frac{n_2 N_1 - n_1 N_2}{n_1 + n_2}(\bar{y}_1 - \bar{y}_2)$$

showing that the two methods provide different estimates with the extent of the difference, depending upon the sizes of the strata, the sample sizes, and the estimates of the sample means. According to Cochran (1977), method 2 works well enough if the sample allocation is proportional because a simple random sample distributes itself approximately proportionally among strata. With proportional allocation $N_1/n_1 = N_2/n_2$; therefore the difference of the two estimators is 0. In our case study, the annual

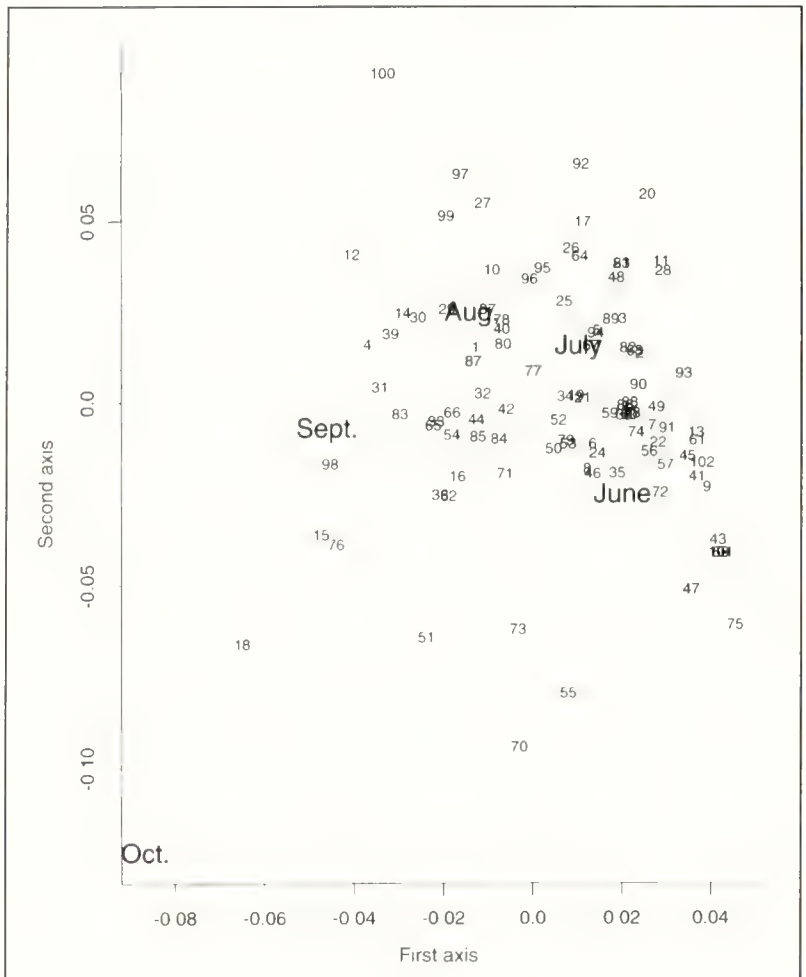

Figure 7

Plots of the determined quantities for sample (anglers) and category (months) from the correspondence analysis for the fishing days of 104 sampled anglers. The numbers in the figure refer to the number of anglers that were sampled .

catch estimates for the season-permit anglers $C^{(s)}$ were the same value for method 1 and method 2. The population size N and the sample size n were in proportion constant throughout the season; therefore $N_t/n_t = N/n$ was same for all strata. The ratio of the variances is

$$\frac{\hat{V}(\hat{Y})}{\hat{V}(\hat{Y}_c)} = \frac{(n_1+n_2)^2\left\{N_1^2\hat{V}(\bar{y}_1)+N_2^2\hat{V}(\bar{y}_2)\right\}}{(N_1+N_2)^2\left\{n_1^2\hat{V}(\bar{y}_1)+n_2^2\hat{V}(\bar{y}_2)\right\}},$$

which also shows that the precision of both methods depends on the sizes of the strata, the sample sizes, and the variance of the sample means. If the allocation is proportional, the variance ratio becomes 1 and the two variances coincide. The objective of stratified surveys is to obtain precise total effort or catch estimates (or both) over the entire season. A proportional sample allocation is recommended, which allows a simple calculation with method 2 and improves precision of estimates at the same time.

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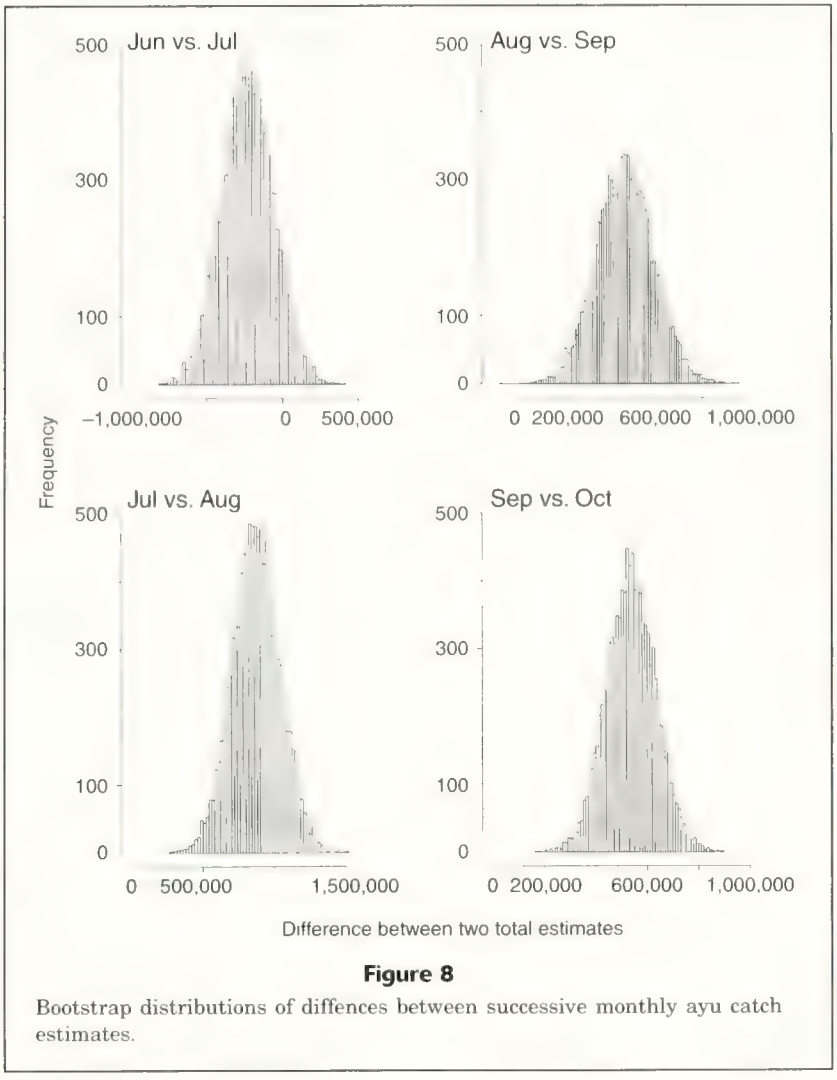

Figure 8

Bootstrap distributions of diffences between successive monthly ayu catch estimates.

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Appendix 1: The covariance of two estimators from sample means

First we consider the covariance of two total estimates. Let X_i and Y_i be simple random samples (i=1, . . . , n) from a population of size N with mean μ_x and μ_y, and $\bar{X}$ and $\bar{Y}$ be two sample means.

Cochran (1977, p .25) derived the covariance of two-sample mean, that is

$$\widehat{\mathrm{Cov}}(\bar{X},\bar{Y}) = \frac{N-n}{N}\frac{1}{n}\widehat{\mathrm{Cov}}(X,Y)$$
$$\frac{N-n}{N^2 n}\sum_{i=1}^{N}(X \quad \mu_x)(Y \quad \mu_y).$$

This is estimated by

$$\widehat{\mathrm{Cov}}(\bar{X},\bar{Y}) = \frac{N-n}{N}\frac{1}{n}\widehat{\mathrm{Cov}}(X,Y)$$
$$\frac{N-n}{Nn(n \quad 1)}\sum_{i}^{n}(X_i - \bar{X})(Y_i - \bar{Y}).$$

The covariance between two population total estimators is defined by

$$\widehat{\mathrm{Cov}}(\hat{X},\hat{Y}) = \widehat{\mathrm{Cov}}(N\bar{X},N\bar{Y}) = E(N\bar{X} - N\mu_x)(N\bar{Y} - N\mu_y)$$
$$N^2\widehat{\mathrm{Cov}}(\bar{X},\bar{Y}) \quad \frac{N(N \quad n)}{n}\widehat{\mathrm{Cov}}(X,Y).$$

This is estimated by

$$\widehat{\mathrm{Cov}}(\hat{X},\hat{Y}) \quad \frac{N(N-n)}{n(n \quad 1)}\sum_{i}(X \quad \bar{X})(Y - \bar{Y}).$$

For the monthly total catches, we get

$$\widehat{\mathrm{Cov}}(\hat{C}_i,\hat{C}_k) \quad \frac{N(N-n)}{n(n \quad 1)}\sum_{i}^{n}(C_i - \bar{C}_i)(C_i - \bar{C}_i).$$

Appendix 2: Approximate covariance between $\hat{W}_k^{(s)}$ and $\hat{W}_{k'}^{(s)}$

Taylor's series of $\hat{W}_k$ with respect to the random variables is obtained by

$$\hat{W}_k = C_i\bar{w}_i + \bar{w}_k(\hat{C}_k - C_i) + C_i(\hat{w}_k - \bar{w}_k).$$

From Taylor's series (mentioned above), the approximate covariance is obtained.

$$\mathrm{Cov}(\hat{W}_k^{(s)},\hat{W}_{k'}^{(s)}) = E(\hat{W}_k^{(s)} - W_k^{(s)})(\hat{W}_{k'}^{(s)} \quad W_{k'}^{(s)})$$
$$\sim E\left[\bar{w}_k(\hat{C}_k^{(s)} - C_k^{(s)}) + C_k^{(s)}(\hat{\bar{w}}_k - \bar{w}_k)\right]$$
$$\left[\bar{w}_{k'}(\hat{C}_{k'}^{(s)} \quad C_{k'}^{(s)}) + C_{k'}^{(s)}(\hat{\bar{w}}_{k'} - \bar{w}_{k'})\right]$$
$$\begin{cases} -\bar{w}_i\bar{w}_{k'}\mathrm{Cov}(\hat{C}_k^{(s)},\hat{C}_{k'}^{(s)}) + \bar{w}_k C_{k'}^{(s)}\mathrm{Cov}(\hat{C}_k^{(s)},\hat{\bar{w}}_{k'}) \\ +C_i^{(s)}\bar{w}_{k'}\mathrm{Cov}(\hat{\bar{w}}_k,\hat{C}_{k'}^{(s)}) + C_k^{(s)}C_{k'}^{(s)}\mathrm{Cov}(\hat{\bar{w}}_k,\hat{\bar{w}}_{k'}). \end{cases}$$

delete ^ carets

Here $\hat{C}_{(\cdot)}^{(s)}$ and $\hat{\bar{w}}_{(\cdot)}$ are independent, and both w_k and $w_{k'}$ are estimated from different samples. Therefore Cov $(\hat{C}_k^{(s)},\hat{\bar{w}}_{k'}) = \mathrm{Cov}(\hat{\bar{w}}_k,\hat{C}_{k'}^{(s)}) = \mathrm{Cov}(\hat{\bar{w}}_k,\hat{\bar{w}}_{k'}) = 0$, then we get the covariance as only the first term.

Appendix 3: Approximate variance of $\hat{R}$

Taylor's series of $\hat{R}$ with respect to $\hat{C}$ and $\hat{M}$ is obtained by

$$\hat{R} = \frac{C}{M} + \frac{1}{M}(\hat{C} \quad C) \quad \frac{C}{M^2}(\hat{M} \quad M).$$

Then the approximate variance is obtained by

$$V(\hat{R}) = E(\hat{R} \quad R)^2 \quad \frac{1}{M^2}V(\hat{C}) + \frac{\hat{C}^2}{M^4}V(\hat{M})$$
$$2\frac{\hat{C}}{M^3}\mathrm{Cov}(\hat{C},\hat{M}).$$

Appendix 4: Covariance between $\hat{C}_k^{(d)}$ and $\hat{C}_{k'}^{(d)}$

By expanding $\hat{C}_k^{(d)}$ and $\hat{C}_{k'}^{(d)}$ we get

$$\hat{C}_i^{(d)} \quad Dp_i R_i + DR_i(\hat{p}_i \quad p_i) + Dp_i(\hat{R}_i - R_i).$$
$$\hat{C}_i^{(d)} \quad Dp_i R_i + DR_i(\hat{p}_k - p_k) + Dp_k(\hat{R}_k - R_k);$$

then the approximate covariance is given by

$$\mathrm{Cov}(\hat{C}_i^{(d)},\hat{C}_k^{(d)}) = E(\hat{C}_i^{(d)} - Dp_i R_i)(\hat{C}_k^{(d)} - Dp_k R_k)$$
$$= D^2\begin{bmatrix} R_i R_k\mathrm{Cov}(\hat{p}_i,\hat{p}_k) + R_i p_k\mathrm{Cov}(\hat{p}_k,\hat{R}_k) \\ +p_i R_k\mathrm{Cov}(\hat{R}_i,\hat{p}_k) + p_i p_k\mathrm{Cov}(\hat{R}_i,\hat{R}_k) \end{bmatrix}.$$

If the first three covariance components are equal to 0 because of independent sampling, then we have

$$\mathrm{Cov}(\hat{C}_i^{(d)},\hat{C}_k^{(d)}) = D^2 p_i p_k\mathrm{Cov}(\hat{R}_i,\hat{R}_k).$$

Here we can write $\hat{R}_k$ and $\hat{R}_{k'}$ as the ratio of two random variables from Equation 1 by

$$\hat{R}_k = \frac{\hat{C}_k^{(s)}}{N\hat{\bar{M}}_k}.$$

By using a method similar to that given in Appendix 3, we get

$$\mathrm{Cov}(\hat{R}_k, \hat{R}_{k'}) = \frac{1}{N^4}\left(\begin{array}{l} \dfrac{1}{\hat{\bar{M}}_k\hat{\bar{M}}_{k'}}\mathrm{Cov}(\hat{C}_k^{(s)}, \hat{C}_{k'}^{(s)}) \\ -\dfrac{\hat{C}_{k'}^{(s)}}{\hat{\bar{M}}_k\hat{\bar{M}}_{k'}^2}\mathrm{Cov}(\hat{C}_k^{(s)}, \hat{\bar{M}}_{k'}) \\ -\dfrac{\hat{C}_k^{(s)}}{\hat{\bar{M}}_k^2\hat{\bar{M}}_{k'}}\mathrm{Cov}(\hat{\bar{M}}_k, \hat{C}_{k'}^{(s)}) \\ +\dfrac{\hat{C}_k^{(s)}\hat{C}_{k'}^{(s)}}{\hat{\bar{M}}_k^2\hat{\bar{M}}_{k'}^2}\mathrm{Cov}(\hat{\bar{M}}_k, \hat{\bar{M}}_{k'}) \end{array}\right).$$

Here $\widehat{\mathrm{Cov}}(\hat{C}_k^{(s)}, \hat{C}_{k'}^{(s)})$ and $\widehat{\mathrm{Cov}}(\hat{\bar{M}}_k, \hat{\bar{M}}_{k'})$ are already given by Equation 18 and Equation 24. Hence we can estimate $\mathrm{Cov}(\hat{C}_k^{(s)}, \hat{\bar{M}}_{k'})$ and $\mathrm{Cov}(\hat{\bar{M}}_k, C_{k'}^{(s)})$. These are the covariances between a total estimate and a sample mean. By a method similar to that in Appendix 1, we have

$$\begin{aligned}\mathrm{Cov}(\hat{X}, \bar{Y}) &= E(N\bar{X} - N\mu_x)(\bar{Y} - \mu_y) \\ &= N\mathrm{Cov}(\bar{X}, \bar{Y}) = \frac{N(N-n)}{n}\mathrm{Cov}(X, Y).\end{aligned}$$

The covariance is estimated by

$$\widehat{\mathrm{Cov}}(\hat{X}, \bar{Y}) = \frac{N-n}{n(n-1)}\sum_{i=1}^{n}(X_i - \bar{X})(Y_i - \bar{Y}).$$

For our case, the two covariances are as follows;

$$\widehat{\mathrm{Cov}}(\hat{C}_k^{(s)}, \hat{\bar{M}}_{k'}) = \frac{N-n}{n^2(n-1)}\sum_{i=1}^{n}(C_{ik} - \hat{\bar{C}}_k)(M_{ik'} - \hat{\bar{M}}_{k'})$$

$$\widehat{\mathrm{Cov}}(\hat{\bar{M}}_k, \hat{C}_{k'}^{(s)}) = \frac{N-n}{n^2(n-1)}\sum_{i=1}^{n}(C_{ik} - \hat{\bar{C}}_{k'})(M_{ik} - \hat{\bar{M}}_k).$$

Physiological ecology of juvenile chinook salmon (*Oncorhynchus tshawytscha*) at the southern end of their distribution, the San Francisco Estuary and Gulf of the Farallones, California*

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Abstract—Juvenile chinook salmon, *Oncorhynchus tshawytscha*, from natal streams in California's Central Valley demonstrated little estuarine dependency but grew rapidly once in coastal waters. We collected juvenile chinook salmon at locations spanning the San Francisco Estuary from the western side of the freshwater delta—at the confluence of the Sacramento and San Joaquin Rivers—to the estuary exit at the Golden Gate and in the coastal waters of the Gulf of the Farallones. Juveniles spent about 40 d migrating through the estuary at an estimated rate of 1.6 km/d or faster during their migration season (May and June 1997) toward the ocean. Mean growth in length (0.18 mm/d) and weight (0.02 g/d) was insignificant in young chinook salmon while in the estuary, but estimated daily growth of 0.6 mm/d and 0.5 g/d in the ocean was rapid ($P \leq 0.001$). Condition (K factor) declined in the estuary, but improved markedly in ocean fish. Total body protein, total lipid, triacylglycerols (TAG), polar lipids, cholesterol, and nonesterified fatty acids concentrations did not change in juveniles in the estuary, but total lipid and TAG were depleted in ocean juveniles. As young chinook migrated from freshwater to the ocean, their prey changed progressively in importance from invertebrates to fish larvae. Once in coastal waters, juvenile salmon appear to employ a strategy of rapid growth at the expense of energy reserves to increase survival potential. In 1997, environmental conditions did not impede development: freshwater discharge was above average and water temperatures were only slightly elevated, within the species' tolerance. Data suggest that chinook salmon from California's Central Valley have evolved a strong ecological propensity for a ocean-type life history. But unlike populations in the Pacific Northwest, they show little estuarine dependency and proceed to the ocean to benefit from the upwelling-driven, biologically productive coastal waters.

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Estuaries are considered important in the development of juvenile salmon. In the Pacific Northwest, estuaries have been shown to provide nursery and rearing conditions for juveniles emigrating from streams of birth to the ocean (Reimers, 1973; Healey, 1982; Levy and Northcote, 1982; Myers and Horton, 1982; Simenstad et al., 1982; McCabe et al., 1986). The San Francisco Estuary is the largest estuary on the West Coast and is a segment in the migration corridor for chinook salmon (*Oncorhynchus tshawytscha*) from natal streams in the watersheds of the Sacramento and San Joaquin Rivers, known as California's Central Valley. The Central Valley is unique by having four runs of chinook salmon which constitute a significant socioeconomic resource. Ocean harvest south of Pt. Arena (estimated as 85–95% from Central Valley stocks) and spawning escapement range between 0.5 and 1.3×10^6 chinook salmon per year (1970–98) and represent about $60 million (U.S.) in personal income annually (PFMC[1]). Beyond the direct value of Central Valley chinook salmon, their demography and welfare significantly affect the financial and societal aspects of water rights decisions.

Chinook salmon populations migrating through the San Francisco Estuary are at the southern limit of the species' geographical range and are subject to the impacts of a highly urbanized, industrialized, and agricultural freshwater and estuarine system (Nichols et al., 1986). All chinook salmon runs originating in the Central Valley are in jeopardy. Before 1900, spawning runs were estimated at 2×10^6 adults (Fisher, 1994), but in 1998 only an estimated 0.25×10^6 returned of which about 30% were of hatchery origin (PFMC[1]). The Sacramento River winter-run chinook was the first Pacific salmonid species listed under the U.S. Endangered Species Act of 1973 (ESA). Originally categorized as threatened in 1989, its status was changed to endangered in 1994. Chinook salmon of the Central Valley spring run, once forming the dominant chinook race in California (Clark, 1929), were listed as threatened in 1999. Even the fall run, by far the dominant run today (92% of all Central Valley spawners, 1990–98 [PFMC[1]]), has uncertain status and is an ESA candidate. Hatchery production supports the natural fall run, and the other runs to a much lesser degree. Annually, about 35 million chinook salmon are produced by state and federal hatcheries in the Central Valley; the fall run comprises 95% (Mills et al., 1997).

California and federal water development projects, such as dams and water diversions, have clearly played a role in the decline of Central Valley salmon (Moyle, 1994), but other factors may al-

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[1] PFMC (Pacific Fishery Management Council). 1999. Review of 1998 ocean salmon fisheries. Pacific Fisheries Management Council, Portland, OR, 65 p. PFMC, 2130 SW Fifth Ave., Suite 224, Portland, OR 97201.

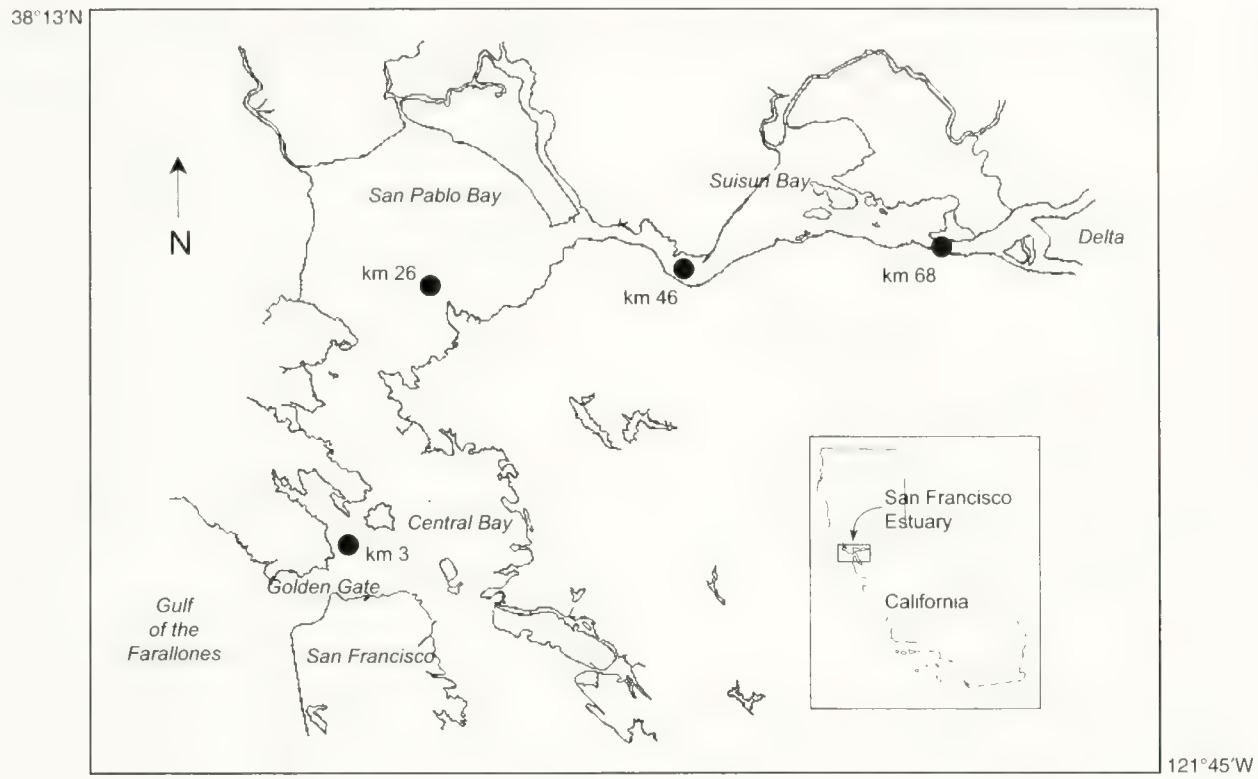

Figure 1

The northern portion of the San Francisco Estuary and nearshore Gulf of the Farallones. Juvenile salmon collection locations are denoted as km (e.g. km 26) from the estuary exit at the Golden Gate. Juvenile salmon were collected throughout the nearshore area in the Gulf of the Farallones, not at specific locations.

so be involved. Migration through the highly impacted San Francisco Estuary and early residence in a marine environment at the southern margin of the species' distribution may impair physiological development that could lead to direct mortality or, indirectly, to reduced survival potential during the oceanic phase.

Although some data exist on abundance, growth, and feeding for chinook salmon migrating through estuaries in southeastern Alaska and British Columbia (Healey, 1980b, 1982; Levy and Northcote, 1982; Landingham et al., 1998); Washington and Oregon (Reimers, 1973; Myers and Horton, 1982; Simenstad, et al. 1982; McCabe et al.,1986; Fisher and Pearcy, 1996); and the Klamath River estuary in northern California (Wallace and Collins, 1997), the only data available for Central Valley emigrants are those of Kjelson et al. (1982). In that paper, life history descriptions were presented for fall-run juveniles, but the emphasis was on fry (≤70 mm fork length) in the freshwater delta at the head of the estuary. Almost nothing is known of juvenile chinook biology in the larger saline portions of the San Francisco Estuary.

Knowledge of juvenile chinook salmon biology during their first year in the marine environment is even more limited, and nonexistent for the area south of the California-Oregon border. Healey (1980a) presented distribution, growth, and feeding information on first ocean-year chinook salmon in the Strait of Georgia, British Columbia. Similar data have been presented for juvenile chinook from the Columbia River drainage off the Oregon and Washington coasts (Miller et al., 1983; Brodeur and Pearcy, 1990; Fisher and Pearcy, 1995).

The purpose of this study was to describe juvenile chinook salmon physiological development during their emigration through the San Francisco Estuary and early residence in the coastal waters of central California. Residence time, age, growth, condition, lipid classes and protein concentrations, and feeding data are presented to characterize the significance of habitat utilization at the southern limit of the species' distribution. The information presented here can serve as a basis for comparison with other year classes from the Central Valley and with populations from more northerly estuaries, as well as for assessments of the influences of natural and anthropogenic perturbations on salmon habitat.

Methods

Study area

Juvenile salmon leaving California's Central Valley pass through the San Francisco Estuary, a series of embayments, before entering the ocean in the Gulf of the Farallones (Fig. 1). The delta, a freshwater network of channels and leveed

islands at the confluence of the Sacramento and San Joaquin Rivers, forms the eastern boundary. Measurable salinity (>1 psu) occurs on the western side of the delta in Suisun Bay. Water flows through Suisun Bay into San Pablo Bay, then into the Central Bay of San Francisco Bay before exiting the estuary at the Golden Gate. The estuary has a surface area of about 1100 km^2 and is fringed on the northern shore with marshes, which have shrunk by more than 90%, to 125 km^2, since 1850 (Conomos, 1979). Most of the estuary shoreline is urban, suburban, and industrial development, however. The Gulf of the Farallones, a relatively broad expanse of the continental shelf extending from Pt. Reyes (38°00′N, 123°01′W) to Pillar Pt. (37°30′N, 122°30′W) to the Farallon Islands (Southeast Farallon Island—37°42′N, 123°00′W) on the edge of the continental shelf, ranges to 90 m but is mostly 20 to 50 m deep. This hydrodynamically complex area is influenced by the cool southerly flowing California Current; freshwater discharge from the San Francisco Estuary; and seasonally strong coastal upwelling (spring and summer) and a northerly flowing countercurrent, the Davidson Current (winter).

Field sampling

Juvenile chinook salmon in this study were collected from the fall run, as determined by the daily length criteria used to discriminate juveniles among the four runs (Johnson et al., 1992). Because salmon from the four runs are phenotypically indistinguishable, to target fall-run juveniles we used daily length criteria and collected fish during the period when fall-run chinook salmon dominate the migration toward the ocean.

We collected juvenile chinook salmon at four locations spanning the San Francisco Estuary (Fig. 1): at km 68, the west side of the delta at the confluence of the Sacramento and San Joaquin Rivers; km 46, the exit from Suisun Bay; km 26 in San Pablo Bay; and several sites within a 1-km radius of km 3 for greater coverage of the estuary exit at the Golden Gate and to avoid ship traffic. Two multiday surveys of the estuary were completed starting at km 68 and proceeding through successive downstream locations to the Golden Gate. The first sampling date was 30 April 1997 at km 68; the last was 15 July 1997 at km 3.

Collections were made in the estuary with a midwater trawl towed at 2–3 knots for 15–30 min. The trawl was made of nylon mesh with a 10-m headrope and footrope, 10-m height at the mouth, and 20-m length. Mesh size was 1.6 cm at the headrope and decreased to 0.4 cm before the codend. The codend was fitted with a 1.27-cm knotless mesh liner. The net was kept open by aluminum spreaders and depressors. For most tows, the spreaders were visible at the surface, confirming that the net fished the upper layer of the water column.

Juvenile chinook salmon were also obtained from the coastal ocean in the Gulf of the Farallones. Stations where salmon were caught were within 15 km of the Golden Gate in waters 18 to 36 m deep. A high-speed midwater rope trawl was towed at 3–4 knots for 15–30 min at each site. The net had a 53-m headrope and footrope with a 1.27-cm mesh codend liner (Dotson and Griffith, 1996). Temperature-depth recorders attached to the footrope and headrope indicated that the net fished 5–10 m below the surface with a vertical opening of 13 m.

Fish were removed from the net as soon as practicable and placed in labeled plastic zip-top bags. Juveniles captured within the estuary were kept under ice: those from the ocean were stored at –80°C, until returned to the laboratory.

We collected hydrologic data during all field trips. Within the estuary, a Hydrolab H20® Multiprobe connected by cable to a Surveyor 3® data logger (Hydrolab Corp., Austin, TX) was used to record vertical profiles of temperature, salinity, dissolved oxygen, pH, and turbidity. In the Gulf of the Farallones, a SeaCat SBE 19-03® (Sea-Bird Electronics, Inc., Bellevue, WA) conductivity-temperature-depth sonde (CTD) recorded profiles of temperature and salinity in a grid of stations spaced at 2′ latitude and longitude intervals encompassing the salmon fishing sites.

Laboratory analyses

In the laboratory, we examined, measured, and dissected fish, usually within 24 h of capture. Fork length and total body weight were recorded. The peritoneal cavity was opened by incision along the ventral side from vent to opercular isthmus. The stomach and its contents were removed and stored in 10% buffered formalin for subsequent analysis of prey. Sagittal otoliths were removed, cleaned of membranes, rinsed in deionized water, and stored for subsequent aging. The remaining portion of the fish was placed in a Whirl® bag, purged with N_2, and stored at –80°C for lipid and protein analyses.

Heads of juvenile salmon containing coded-wire tags, evident by a missing adipose fin, were removed and sent to the U.S. Fish and Wildlife Service, Stockton, CA, to obtain data on the location and time of release of each fish.

Concentrations of lipid classes and total protein were determined in 15 fish randomly chosen from each location. Heads, fins, and stomachs were removed to limit analyses to body constituents. Frozen bodies were minced with a knife, then homogenized in a blender for about 30 sec to a uniform paste. We extracted lipids from a 1g- to 3g-aliquot by using the method of Bligh and Dyer (1959). Total lipid was quantified by thin-layer chromatography with flame-ionization detection with an Iatroscan TH-10 Mark V® (Iatron Laboratories, Inc., Tokyo, Japan) according to procedures published previously (MacFarlane et al., 1990, 1993). Total lipid was separated into steryl or wax ester, triacylglycerols, nonesterified fatty acids, cholesterol, and polar lipid classes and quantified according to methods in MacFarlane and Norton (1999). We estimated total protein concentration by the Lowry method, using bovine serum albumin as a standard (Lowry et al., 1951). All lipid and protein values are expressed as wet weight (mg/g).

Fish ages were estimated from otolith analysis (Brothers, 1987). Sagittae were embedded in epoxy, then ground and polished on the distal surface to a mid-sagittal section. Otolith concentric bands were counted under oil immersion with transmitted polarized light illumination into a video microscopy system at a monitor magnification

of 1500×. Counts representing daily increments of growth were made from the otolith margin (dorsal edge) to a posterior primordium. Each otolith was counted at least two times by the same reader. Data are presented as age, in days, between the hatching check and the otolith margin.

Stomach contents were identified and quantified according to methods of Hobson and Chess (1976). Prey were identified to the lowest possible taxa, enumerated, and their relative volume and size distribution recorded. The derived parameter, index of relative importance (IRI), was used to determine the importance of specific taxa to juvenile salmon at each sampling location. The IRI was computed by the equation

$$IRI = (N + V)FO,$$

where N, V, and FO = the percent number, volume, and frequency of occurrence, respectively, of a taxon in the stomach contents (Pinkas et al., 1971).

Size, age, condition, lipids, and protein data were analyzed for variability among locations by means of the general linear model of analysis of variance. Differences among specific locations were determined with Tukey's studentized range test, set at $\alpha = 0.05$, which controls for MEER (maximum experimentwise error rate) under complete or partial null hypotheses. All statistical procedures were performed with SAS software (SAS Institute, Inc., 1994).

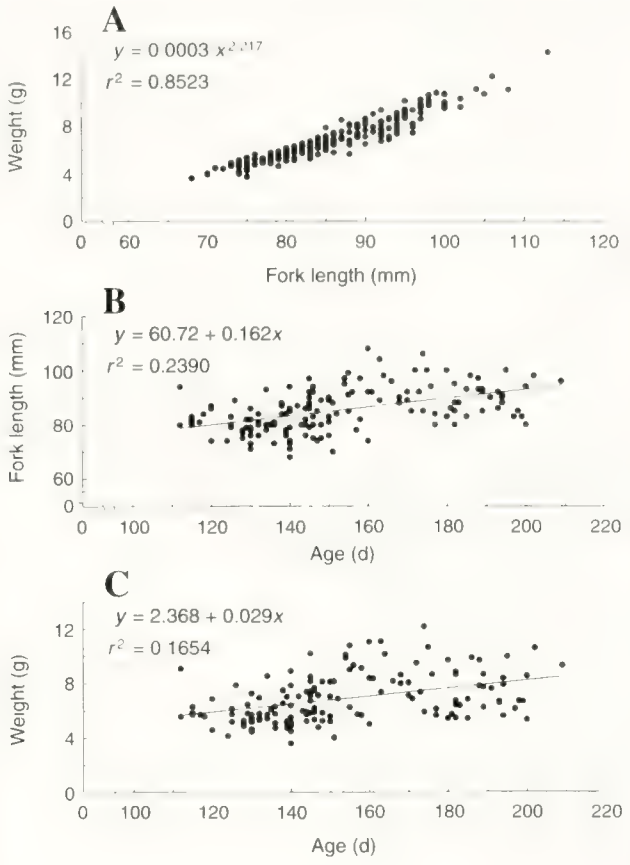

Figure 2

Fork lengths, weights, and ages of all juvenile chinook salmon collected from the San Francisco Estuary and Gulf of the Farallones: (**A**) fork length-weight relationship; (**B**) age-fork length relationship; (**C**) age-weight relationship.

Results

We collected and evaluated 310 subyearling chinook salmon from the 1996–97 year class. The catch consisted of naturally spawned and hatchery-produced fish of unknown proportions because less than 3% were marked (by adipose fin clips and coded wire tags) and there were no morphological features to distinguish hatchery from naturally produced salmon. Mean fork length (FL) was 89 mm and ranged from 68 to 113 mm. Total body weights ranged from 3.59 to 14.62 g, with a mean of 7.58 g. A power function was fitted to the relationship between FL and weight (Fig. 2A). Ages were determined for 156 juveniles and ranged from 112 to 209 days after hatching. The relationship of FL or weight to age was not as well fitted as that for weight on FL (Fig. 2, B and C); however, length and weight were positively correlated to age ($P<0.0001$).

Each sampling location within the estuary was visited more than once on successive surveys through the 30 April–15 July period of juvenile emigration. There were no statistically significant trends in size, age, lipid, and protein variables by sampling date at any location; therefore we combined data for each location from both surveys through the estuary.

While in the estuary, juvenile chinook salmon grew little in length or weight; but in coastal waters, they grew rapidly (Fig. 3). Juveniles entering the estuary at km 68 had a mean (±SE) FL of 82.8 ±0.7 mm and weight of 6.36 ±0.21 g. At the exit of the estuary (km 3), mean FL and weight of cohorts were 89.5 ±1.1 mm and 7.23 ±0.30 g, representing mean gains of about 7 mm and 0.9 g. Size changes within the estuary were not statistically significant ($P>0.05$). Year-class cohorts in the coastal waters of the Gulf of the Farallones were significantly longer and heavier than those from the estuary (FL, $P<0.0001$; weight, $P<0.001$). Ocean-caught juveniles were 8.2 mm longer and weighed 6.5 g more than fish collected near the estuary exit.

Juvenile salmon spent about 40 d migrating along the 65-km length of the estuary, according to otolith increment counts (Fig. 3C). Mean age at the entry to the estuary was 136 ±2 d; at the exit it was 176 ±3 d. Juveniles aged from the Gulf of the Farallones were 156 ±5 days old, indicating a shorter freshwater or estuarine residence than that for those captured from the Golden Gate area.

Daily growth rates in the estuary can be calculated from differences in mean size over the 40-d estimated time of

transit. According to this technique, mean daily growth was about 0.18 mm/d and 0.02 g/d.

Because we aged only a subset of fish from each sampling location, mean age of all fish obtained at each site could be estimated with the FL-on-age regression equation for age (Fig. 2B). Results of that computation revealed close agreement with measured ages at all locations except the Gulf of the Farallones (Fig. 3C), where calculated age was 189 ±8 d. Both methods of age determination indicated that juveniles caught in coastal waters were from the same year class.

The average migration rate through the estuary was estimated at 1.6 km/d on the basis of the difference between mean ages of juvenile salmon sampled at the estuary entry and exit (i.e. 65 km/[176 d at km 3 –136 d at km 68]). Data from coded-wire–tagged fish caught within the estuary and the Gulf of the Farallones revealed a wide range of migration rates (Table 1). For those captured within the estuary (17 of 24), the mean migration rate was 4.0 ±0.9 km/d. Most tagged-recaptured salmon had rates ≤2.6 km/d but were from two releases within the estuary, thus representing migration rates in the lower estuary only. Juveniles released farther upstream in the rivers and caught in the lower estuary had somewhat faster migration rates (x=9.1 ±2.5 km/d, n= 4).

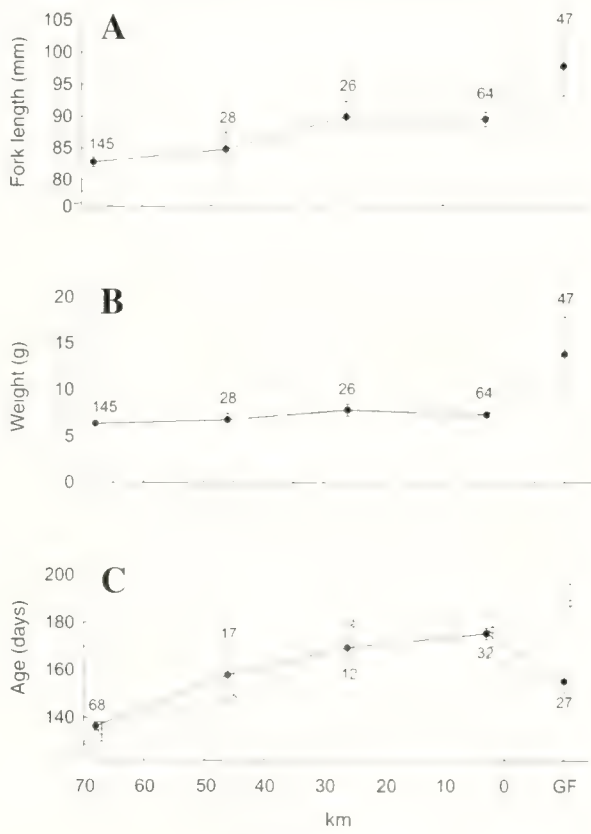

Figure 3

Mean (±SE) fork lengths (**A**), weights (**B**), and ages (**C**) of juvenile chinook salmon collected from locations in the San Francisco Estuary (km 68, km 46, km 26, km 3) and the Gulf of the Farallones (GF). Open circles and dashed line in (C) represent calculated ages of all fish at each location from regression of fork length on age from Figure 2(B). Numbers near means are sample sizes.

Not only did juvenile chinook salmon grow slowly while in the estuary, their condition declined as they proceeded to the Golden Gate (Fig. 4). There was a significant decrease in Fulton's condition factor (K) between fish entering the estuary and those departing (P<0.001). Once the fish were in coastal waters, however, their condition improved markedly.

Body constituents and energy reserves varied little while migrating fish were in the estuary, but total lipid was depleted in fish from the Gulf of the Farallones (Fig. 5A). Total body protein concentrations were approximately 150 mg/g, wet weight, in fish from all locations, and did not vary significantly. Total lipid also did not vary in fish within the estuary but was significantly lower in salmon caught in the ocean (P<0.0005). Mean lipid concentration for fish in the estuary was about 30 mg/g, or 15% of dry weight, and decreased to 17.7 ±1.6 mg/g in the ocean. The decline in lipids in fish from the Gulf of the Farallones was attributed to decreased concentrations of triacylglycerols (TAG), the dominant lipid class (Fig. 5B). TAG levels increased from 14.8 ±2.5 mg/g in fish entering the estuary to about 18 mg/g in estuarine salmon and were depleted to 4.3 ±1.4 mg/g in coastal fish. The concentration of polar lipids, composed primarily of phospholipids, remained unchanged through the estuary and in the ocean. Other lipid classes—cholesterol and nonesterified fatty acids—were found at much lower concentrations and did not vary significantly during the emigration. Steryl or wax esters were absent or at very low levels in most individuals and showed no differences related to location.

We examined feeding and prey selectivity in juvenile chinook salmon migrating through the estuary and in coastal waters. A lesser proportion of fish leaving the rivers contained food items compared with those within the estuary. Fifty percent of juvenile salmon had stomach contents at Chipps Island (km 68, 21 of 42 sampled). In contrast, more than 80% from Carquinez Strait (km 46, 8 of 10 samples) and San Pablo Bay (km 26, 20 of 23 samples) had prey in their stomachs. A lower percentage (70%) from the Central Bay (km 3, 9 of 13) had fed recently, but in the Gulf of the Farallones, 82% (23 of 28) of the juveniles contained food.

The relative importance of prey items varied as juvenile salmon migrated through the estuary and entered the ocean (Table 2). Stomachs of juveniles leaving the rivers contained primarily gammaridean amphipods *Corophium* sp., and lesser amounts of crab megalopae, dipteran insects, other malacostracan crustaceans, and other insects. After the salmon passed through Suisun Bay (km 46), their stomachs contained mostly the hemipteran *Hesperocorixa* sp., the calanoid copepod *Eucalanus californicus*, the mysid *Acanthomysis* sp., fish larvae, and other insects. Cumaceans were clearly dominant in juvenile salmon in San Pablo Bay (km 26), but

Table 1

Minimum distance traveled by coded-wire tagged juvenile chinook salmon between marking and recapture.

Release			Capture					
Date	Location	km	Date	Location	km[1]	Km traveled	Days free	Km/d traveled
1 Apr 1997	Battle Creek	470	12 May 1997	Gulf of Farallones	−19	489	41	11.93
15 Apr 1997	West Sacramento	157	9 May 1997	Gulf of Farallones	−19	176	24	7.33
16 Apr 1997	Battle Creek	470	11 May 1997	Gulf of Farallones	−17	487	25	19.48
24 Apr 1997	Gridley Boat Ramp	244	29 May 1997	Pt. San Pablo	17	227	35	6.49
24 Apr 1997	San Pablo Bay	37	10 May 1997	Gulf of Farallones	−22	59	16	3.69
24 Apr 1997	Gridley Boat Ramp	244	11 May 1997	Gulf of Farallones	−20	264	17	15.53
28 Apr 1997	Mossdale	150	12 May 1997	Gulf of Farallones	−20	170	14	12.14
29 Apr 1997	Dos Reis Park	146	27 May 1997	Carquinez Strait	46	100	28	3.57
29 Apr 1997	Dos Reis Park	146	11 May 1997	Gulf of Farallones	−20	166	12	13.83
14 May 1997	Hatfield State Park	221	29 May 1997	Pt. Pinole	26	195	15	13.00
19 May 1997	Benicia	43	29 May 1997	Pt. Pinole	26	17	10	1.70
19 May 1997	Benicia	43	29 May 1997	Pt. Pinole	26	17	10	1.70
19 May 1997	Benicia	43	29 May 1997	Pt. San Pablo	17	26	10	2.60
19 May 1997	Benicia	43	29 May 1997	Pt. San Pablo	17	26	10	2.60
19 May 1997	Benicia	43	29 May 1997	Pt. San Pablo	17	26	10	2.60
19 May 1997	Benicia	43	29 May 1997	Pt. San Pablo	17	26	10	2.60
19 May 1997	Benicia	43	29 May 1997	Pt. San Pablo	17	26	10	2.60
19 May 1997	Benicia	43	29 May 1997	Pt. San Pablo	17	26	10	2.60
19 May 1997	Benicia	43	29 May 1997	Pt. San Pablo	17	26	10	2.60
19 May 1997	Benicia	43	29 May 1997	Pt. San Pablo	17	26	10	2.60
19 May 1997	Benicia	43	29 May 1997	Pt. San Pablo	17	26	10	2.60
19 May 1997	Benicia	43	29 May 1997	Pt. San Pablo	17	26	10	2.60
30 May 1997	Woodbridge Dam	149	Jun 10 1997	Golden Gate	0	149	11	13.55

[1] Negative km data represent distance captured seaward of the Golden Gate.

insects were still important. In the Central Bay, the final embayment before the estuary exit, fish larvae were the dominant forage item. *Ampelisca abdita*, a gammaridean amphipod, and cumaceans were important as well. Fish larvae continued to be the most important prey of juvenile chinook salmon in the coastal waters of the Gulf of the Farallones, but euphausiids and decapod early life stages were also consumed in significant numbers.

Discussion

Chinook salmon from California's Central Valley streams have a largely ocean-type life history although perhaps a few spring and late-fall run juveniles overwinter in freshwater and migrate to the ocean as yearlings (Fisher, 1994; Myers et al., 1998). Fry (<70 mm FL) are abundant in the freshwater delta from February to April. They leave as smolts (>70 mm FL) and enter the San Francisco Estuary, primarily in May and June. Kjelson et al. (1982) reported that few juveniles were present in the delta or estuary

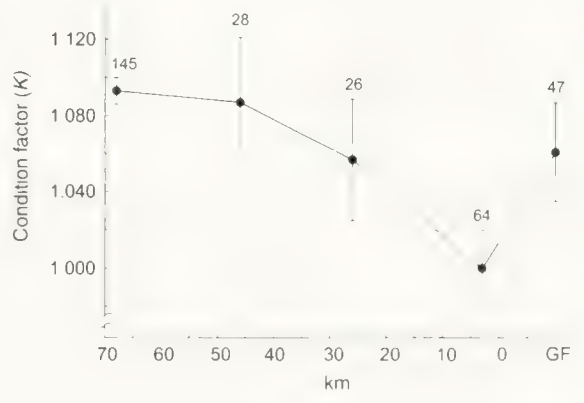

Figure 4

Changes in mean (±SE) Fulton's condition factor (*K*) of juvenile chinook salmon from locations in the San Francisco Estuary (km 68, km 46, km 26, km 3) and the Gulf of the Farallones (GF). Numbers above means are sample sizes.

after June. Our findings concur: the smallest salmon we caught was 68 mm FL, and we caught no fish after 27 June. Juveniles were approximately 4.5 months old (after hatching) when they entered the San Francisco Estuary. They spent about 40 days there, migrating at 1.6 km/d, based on mean age differences of fish entering the estuary and fish leaving at the Golden Gate. This is probably a minimum estimate of migration rate, because data from tagged fish caught within the estuary showed rates of 1.70 to 13.55 km/d, representing residence times of 38 to 5 days. A previous mark-recapture study also found higher migration rates (10 to 18 km/d), although the data were for passage through the upstream delta (Kjelson et al., 1982).

Studies in the Pacific Northwest suggest that juveniles of ocean-type chinook salmon make extensive use of estuaries, spending as much as 6 to 9 months in them feeding and growing (Myers and Horton, 1982; Simenstad et al., 1982; Healey, 1991). In the Columbia River estuary, subyearling chinook salmon were present throughout the year, although most abundant in May to September (McCabe et al., 1986). Fall-run juveniles entered the Sixes River estuary in the spring and were abundant from June through August (Reimers, 1973). Juvenile chinook salmon resided in Washington estuaries for 6 to more than 29 weeks, but some individuals were present for up to 189 d (Simenstad et al., 1982). Even in northern California's Klamath River estuary, juvenile fall-run chinook salmon remained from June to September (Wallace and Collins, 1997). The relatively short period of abundance in the San Francisco Estuary and emigration rates presented here suggest that juvenile chinook from the Central Valley may derive less benefit from estuarine residence than do more northerly populations.

Juvenile chinook salmon grew little while in the San Francisco Estuary. Though growth was not statistically significant, on average they increased in size by 7 mm FL and 0.9 g, representing daily growth of 0.18 mm/d and 0.02 g/d. These estimates indicate slower growth than has been reported for juvenile chinook in most estuaries to the north. In five estuaries on Vancouver Island and the Fraser River, juveniles grew 0.21 to 0.62 mm/d (Levy and Northcote, 1982; Healey, 1991). Growth measurements from population sampling and from following marked fish produced similar results in the Sixes River estuary, where daily growth ranged from 0.07 mm/d in summer to 0.9 mm/d in spring (Reimers, 1973). Reimers speculated that the very slow growth during summer was due to food limitation caused by high salmon abundance.

Growth can also be inferred by the change in size of fish collected at the same locations from the beginning to the end of the emigration period. We found no significant increase in size at given locations within the estuary during the May–June emigration season. Kjelson et al. (1982) also found no change in smolt size in the delta from April to June. In contrast, the mean size of juvenile chinook salmon in the Columbia River estuary increased from March to December, suggesting substantial growth or immigration of larger fish during the season.

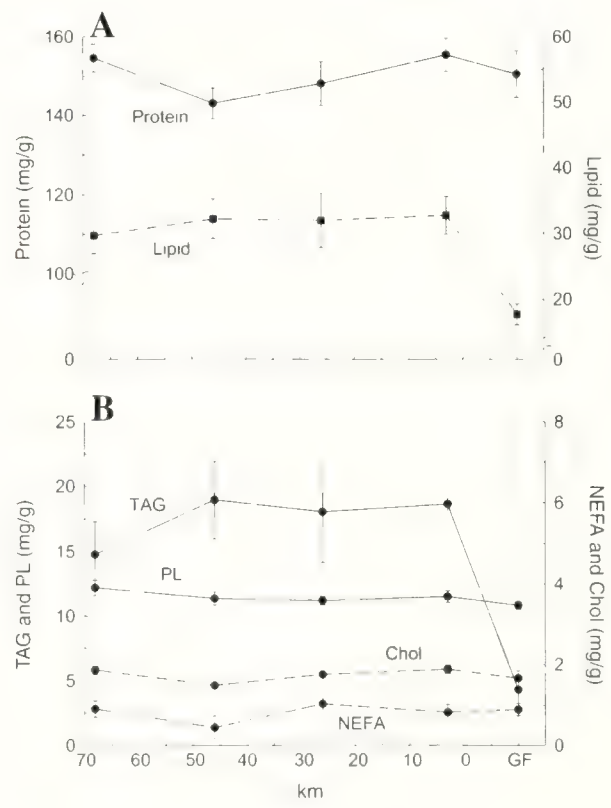

Figure 5

(**A**) Protein and total lipid concentrations, and (**B**) lipid class concentrations (triacylglycerols [TAG], polar lipids [PL], cholesterol [Chol], and nonesterified fatty acids [NEFA]) in juvenile chinook salmon from locations in the San Francisco Estuary (km 68, km 46, km 26, km 3) and the Gulf of the Farallones (GF). Concentrations are mg/g wet weight.

Although little growth occurred during estuarine residence, growth was rapid in the coastal waters of the Gulf of the Farallones. Juvenile ocean cohorts were 10% longer in mean FL and 90% heavier than those from the estuary, although size varied more in ocean residents than in chinook salmon within the estuary. Faster growth rates of juvenile chinook salmon in coastal waters than in estuaries have been reported from British Columbia (Healey, 1980a), and Oregon and Washington (Miller et al., 1983; Fisher and Pearcy, 1995), with rates of 1 mm/d and more. Daily growth rates of juveniles in the Gulf of the Farallones were difficult to determine because the mean age of the subset aged by otolith analysis was less than the mean age of fish at the estuary exit. But if the calculated age of ocean juveniles (from the regression of age on FL) is used, during the calculated 13 d of ocean residence they grew at about 0.6 mm/d and 0.5 g/d, well above rates while in the San Francisco Estuary.

Growth rate estimates from the regressions of FL or weight on age for all juveniles from both the estuary and gulf were 0.16 mm/d and 0.029 g/d. These results agree

Table 2

Stomach contents of juvenile chinook salmon. *%N* is the numerical percentage; *%V* is the percent relative volume; *%FO* is the frequency of occurrence percentage; and *IRI* is the index of relative importance, *(%N + %V)%FO*.

Location and prey species	%N	%V	%FO	IRI
km 68, Chipps Island (*n*=21)				
Malacostraca				
Decapoda				
Caridean shrimp	2.6	5.7	4.8	39.3
Crab megalopae	7.7	10.0	19.0	336.3
Mysidacea				
Unidentified	7.7	4.6	14.3	175.9
Amphipoda				
Gammaridea	2.6	5.7	4.8	39.8
Corophium spp.	30.8	26.4	33.3	1905
Eusirdae unidentified	2.6	5.7	4.8	39.8
Isopoda				
Gnorimosphaero luta	2.6	0.6	4.8	15.4
Insecta				
Hymenoptera				
Unidentified	2.6	5.7	4.8	39.8
Homoptera				
Aphid	2.6	0.3	4.8	13.9
Diptera				
Flies unidentified	2.6	1.1	4.8	17.8
Culicidae	2.6	2.6	4.8	25.0
Unidentified	7.7	6.3	19.0	266.0
Unidentified	10.3	9.7	14.3	286.0
Algae				
Unidentified	5.2	11.4	9.5	157.7
Unidentified	7.7	4.0	4.8	56.2
km 46, Carquinez Strait (*n*=8)				
Malacostraca				
Mysidacea				
Acanthomysis spp.	3.9	17.0	12.5	257.5
Unidentified	2.0	6.0	12.5	100.
Amphipoda				
Gammaridea	3.9	3.0	12.5	86.3
Cumacea	5.9	5.0	12.5	136.3
Copepoda				
Calanoida				
Eucalanus californicus	5.9	15.0	12.5	261.3
Insecta				
Coleoptera				
Unidentified	2.0	14.0	12.5	200.0
Hemiptera				
Hesperocorixa spp.	72.5	1.0	12.5	918.8
Unidentified	2.0	20.0	12.5	275.0
Pisces				
Unidentified	2.9	19.0	12.5	273.8
km 26, San Pablo Bay (*n*=20)				
Crustacean				
Unidentified		2.9	5.0	
km 26, San Pablo Bay (*n*=20) *continued*				
Malacostraca				
Decapoda				
Crab megalopae	0.5	0.3	35.0	28.0
Mysidacea				
Unidentified	0.5	0.5	5.0	5.0
Cumacean				
Unidentified	61.7	17.9	50.0	3980
Amphipoda				
Gammaridea				
Ampelisca abdita	1.6	1.2	10.0	28.0
Corophium spp.	3.6	23.2	5.0	134.0
Corophium spinicorne	0.5	4.2	5.0	23.5
Maera spp.	0.5	1.5	5.0	10.0
Unidentified	1.0	1.3	3.6	8.3
Cirripedia				
Thoracic				
Barnacle cirri	1.6	1.3	10.0	29.0
Insecta				
Coleoptera				
Unidentified	1.0	1.1	5.0	10.5
Hemiptera				
Unidentified	0.5	0.5	5.0	5.0
Homoptera				
Flatidae	0.5	0.3	5.0	4.0
Diptera				
Unidentified	1.6	1.0	15.0	39.0
Lepidoptera	1.3	1.0	5.0	11.5
Orthoptera	0.5	0.3	5.0	4.0
Unidentified	10.4	12.7	25.0	577.5
Polychaeta				
Phyllodocida				
Nereidae	1.0	4.7	10.0	57.0
Unidentified	1.6	8.2	15.0	147.0
Pisces				
Unidentified larvae	0.5	2.4	5.0	14.5
Unidentified	0.5	1.6	5.0	10.5
Algae				
Unidentified	8.8	8.7	30.0	10.5
Unidentified	0.5	0.3	5.0	4.0
km 3, Central Bay (*n*=10)				
Crustacean				
Unidentified		1.2	10.0	
Malacostraca				
Decapoda				
Crab megalopae	1.2	0.1	10.0	13.0

continued

Table 2 (continud)

Location and prey species	%N	%V	%FO	IRI
km 3, Central Bay (n=10) *continued*				
Cumacean				
Unidentified	45.1	11.1	20.0	1124
Amphipoda				
Gammaridea				
Ampelisca abdita	20.7	8.6	60.0	1758
Copepoda				
Siphonostomatoida	1.2	1.2	10.0	24.0
Cirripedia				
Thoracica				
Barnacle cirri	1.2	1.2	10.0	24.0
Insecta				
Unidentified	8.5	1.2	20.0	194.0
Polychaeta				
Phyllodocida				
Nereidae	1.2	2.5	10.0	37.0
Unidentified	1.2	3.7	10.0	49.0
Pisces				
Unidentified larvae	14.6	55.4	60.0	4200
Unidentified	1.2	10.5	10.0	117.0
Algae				
Unidentified	3.7	3.1	10.0	68.0
Gulf of the Farallones (n=23)				
Gastropoda	0.3	0.2	4.3	2.2
Malacostraca				
Decapoda				
Cancer magister (juv)	1.5	6.9	26.0	218.4
Crab megalopae	2.1	7.3	21.7	204.0
Crab zoea	6.8	6.6	26.0	348.4
Caridean shrimp	0.9	1.2	13.0	27.3
Euphausiacea				
Thysanoessa gregaria	6.2	2.6	13.0	114.4
Unidentified	24.9	18.5	47.8	2075
Amphipoda				
Caprella californica	0.3	—	4.3	—
Insecta				
Coleoptera				
Unidentified	0.3	0.3	8.7	5.2
Hymenoptera				
Unidentified	2.1	1.2	8.7	2.3
Homoptera				
Aphid	2.1	0.9	17.4	52.2
Diptera				
Culicidae	0.3	0.1	4.3	1.7
Unidentified	5.3	3.7	21.7	195.3
Arachnida				
Araneae				
Unidentified	0.3	0.2	4.3	2.2
Polychaeta				
Phyllodocida				
Nereidae	0.3	0.5	4.3	3.4
Pisces				
Unidentified larvae	46.3	49.9	70.0	6545

well with growth estimated by differences in mean values at the entrance and exit of the estuary.

Further evidence that residence in the San Francisco Estuary was not beneficial to juvenile salmon was their decline in condition (K-factor) while migrating through the estuary. But, along with faster growth, condition improved markedly in juveniles in coastal waters. Changes in K can be due to several causes, including stomach fullness and metabolic state. In an associated study of contaminants, the weight of stomach contents was measured at the same locations and dates as the ones described here. Stomach contents were 0.5% ±0.1% of body weight in fish with food in their stomachs at both the entrance and exit of the estuary (MacFarlane, unpubl. data). Further, a greater proportion of fish contained food at the estuary exit, where K was the lowest. Thus, differences in stomach fullness were not the cause of lower condition. Changes in metabolic equilibria, reflected in altered body composition of protein and lipids, can change body density, as shown by Brett et al. (1969) for juvenile sockeye salmon (*Oncorhynchus nerka*) and thus affect condition. In juveniles in the San Francisco Estuary, body protein and total lipid concentrations were similar at all sampling locations, so changes in body density were unlikely contributors to reduced condition. However, metabolic costs of smoltification can cause changes in length – weight relationships. During the transformation, salmon can become more slender due to depleted energy reserves (Hoar, 1988), especially TAG (Henderson and Tocher, 1987). It is possible that decreased lipid and protein content, and not changes in relative concentrations, caused by catabolism for seawater adaptation, resulted in juveniles leaving the estuary at a lower weight for a given length than when they first entered. However, in a study conducted in 1999, gill Na^+, K^+-ATPase activity, an indicator of seawater adaptation, was greater in juvenile chinook salmon caught at the entrance to the estuary (km 68) compared with that of those sampled within the rivers leading into the estuary, but was not increased further in those collected at locations within the San Francisco Estuary.[2] This suggests that adaptation was largely completed by the time of estuary entrance and may not be the primary contributor to the body lower condition of fish

[2] Alonzo, J. J., and R. B. MacFarlane. 1999. Unpubl. data. Santa Cruz Laboratory, Southwest Fish. Sci. Ctr. NMFS, NOAA. 110 Shaffer Road, Santa Cruz, CA 95060.

leaving the estuary. Further, Zaugg and McLain (1972) showed that condition was either unchanged or declined for several months after stabilization of higher Na^+, K^+-ATPase levels in salmonids undergoing parr-smolt transformation. The increase in *K*-factor in fish captured in the coastal waters of the Gulf of the Farallones argues against smoltification as the main cause of lower condition in juvenile salmon leaving the estuary.

Although total lipid concentrations were unchanged in juveniles within the estuary, they declined greatly in salmon in the Gulf of the Farallones. Most of the decrease was due to depletion of TAG. It appears that the rapid growth of juveniles in the ocean was fueled by TAG energy reserves acquired during downstream migration. Growth seems to take precedence over maintenance of energy reserves. Increased body lipid (presumably TAG) at the time of ocean entry has been shown to improve juvenile chinook survival (Burrows, 1969; Higgs et al., 1992); thus a lack of substantial TAG accumulation while in the estuary may compromise early ocean survival should prey be scarce.

There was little difference in protein concentrations in juveniles from the estuary and the gulf. This is not surprising: protein appears to be conserved except during periods of starvation. Protein levels in juvenile salmonids have been shown to be unaffected by ration, growth, environmental variation (Shearer et al., 1997; Edsall et al., 1999), or locomotion (Alsop and Wood, 1997).

As juvenile chinook salmon migrated through the San Francisco Estuary, their feeding changed progressively from invertebrates to fish larvae. Young salmon leaving the freshwater delta had recently eaten primarily *Corophium*, which seems also to be a major prey of juvenile chinook in Oregon estuaries (Reimers, 1973; McCabe et al., 1986). In 1979–80, juvenile chinook in the delta preyed primarily on cladocerans and dipterans (Kjelson et al., 1982). Over the past several decades, the zooplankton community in the delta and estuary has changed dramatically because of water diversions and introductions of many exotic species (Kimmerer and Orsi, 1996; Cohen and Carlton, 1998). The change in prey found in our study may be a result of anthropogenic alterations in the ecosystem.

There was greater diversity in feeding in the upper bays—Suisun and San Pablo—where insects, copepods, mysids, and cumaceans formed a major portion of young chinook salmon diet. These embayments are bordered by the last remaining extensive brackish and salt marshes in the northern estuary. Additionally, Suisun Bay includes the mixing zone of fresh and salt water, a well-known locale of high plankton abundance. Thus the high biological productivity of these habitats could be expected to provide diverse food items. The composition of the diet here was similar to that found in more northerly estuaries (Healey, 1991) and provided further evidence that juvenile chinook salmon feed on about the same prey types in these habitats throughout their range.

Chinook salmon are highly piscivorous. Fish larvae were clearly the dominant prey in central San Francisco Bay and in the Gulf of the Farallones. Typically young chinook eat mostly fish larvae as they grow and enter marine environments (McCabe et al., 1986; Fisher and Pearcy, 1996; Landingham et al., 1998). In the coastal waters of the Gulf of the Farallones, juvenile chinook salmon fed on early life stages of euphausiids and decapods as well, but to a lesser extent than on fish. Fish, euphausiids, and decapods were the major prey in coastal ecosystems from Oregon to southeastern Alaska (Brodeur and Pearcy, 1990; Landingham et al., 1998).

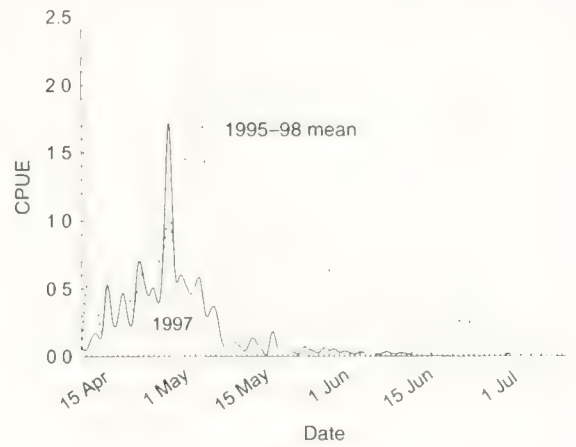

Figure 6

Juvenile chinook salmon catch by midwater trawl at the entrance to the San Francisco Estuary (km 68) in 1997 compared with 1995–98 mean. Catch per unit of effort (CPUE) is presented as the number of salmon/1000 m^3 water. Data from U.S. Fish and Wildlife Service, Stockton, CA.

Once juvenile chinook entered the ocean, feeding intensity appeared to increase. Whereas stomach contents were 0.5% of body weight in the estuary, in the gulf they were 0.9% ±0.1% of body weight. The rapid growth rate found in young salmon shortly after ocean entry seemed to result from greater feeding activity in combination with the utilization of lipid reserves to fuel the synthesis of formed tissues.

To understand the context of data on juvenile salmon physiological ecology, it is helpful to know the relative abundance of these fish and the environmental conditions in 1997. Emigrating juvenile salmon abundance is monitored at the estuary entrance (km 68) by a consortium of California and federal research agencies (Interagency Ecological Program). Data for 1997 indicated that abundance was lower and migration to the ocean occurred earlier than the 1995–98 average (Fig. 6). Mean daily catch per unit of effort (1 January to 30 June 1997) was 0.132 ±0.02 juveniles/(10^3/m^3 water), about 80% less than in 1996 and 1997 and 50% less than in 1998. Freshwater outflow from the delta into the estuary in 1997 was categorized by California Department of Water Resources as "above normal" and peak flows occurred in January, earlier than typical (Fig. 7). Hydrologic conditions in the estuary during May and June 1997 were similar to long-term means, but water temperatures and salinities were statistically higher ($P<0.0001$, Table 3). Water temperatures were 18.4°C,

Table 3

Mean hydrologic characteristics of the water column in the San Francisco Estuary and the coastal Gulf of the Farallones during juvenile chinook salmon migration toward the ocean in 1997 compared with long-term means. Data are means (±SE) of surface to bottom for May and June. Years for long-term mean were 1989–97, except for turbidity and pH, which were 1995–98. (Long-term data for estuary are from U. S. Geological Survey, Menlo Park, CA, and for gulf from Groundfish Population Analysis, Santa Cruz Laboratory, NMFS, Santa Cruz, CA).NTU = nephelometric turbidity units.

	Estuary		Gulf	
Variable	1997	Long-term	1997	Long-term
Temperature(°C)	18.4 (0.1)[1]	17.5 (0.0)	10.6 (0.0)[1]	10.1 (0.0)
Salinity (‰)	16.7 (0.5)[1]	14.7 (0.2)	33.6 (0.0)	33.6 (0.0)
Dissolved O_2 (mg/L)	7.98 (0.03)[2]	7.91 (0.02)		
Turbidity (NTU)	36.0 (3.0)	35.1 (2.8)		
pH	7.58 (0.01)[1]	7.62 (0.00)		
Chl *a* (µg/L)	3.19 (0.05)	3.11 (0.03)		

[1] P (probability of no difference from long-term mean) <0.0001
[2] P<0.05

about 1°C warmer than long-term means, although well within the tolerance limits for the species at these latitudes (Baker et al., 1995). This temperature has been shown to allow growth rates of about 1% body weight/day in juvenile chinook salmon under simulated field feeding conditions (Weatherley and Gill, 1995).

Water flows and temperature are two primary environmental variables affecting the distribution and development of fishes; thus it is reasonable to assume that the timing of the emigration in 1997 was a function of that year's hydrology. Flow and temperature were believed to influence the migration and distribution of juvenile chinook salmon in the Sacramento and San Joaquin Rivers (Kjelson et al., 1982) and other systems (Cramer and Lichatowich, 1978; Healey, 1980b; Wallace and Collins, 1997). In fact, higher water temperatures of the Central Valley drainage may be a factor in the early emigration and physiological development seen in California chinook salmon in contrast to northerly populations (Healey, 1991). Mean water temperature between 1988 and 1997 at the estuary entrance (km 68) was 19.9°C in June and 21.7°C in July,[3] within the range of predicted 10% mortality estimated with a fitted model (Baker et al., 1995). Temperatures within the Central Bay through July, however, remained below 18°C.

The strongest El Niño of the century began in 1997 and may have influenced the physiology and ecology of salmon in the coastal waters of the Gulf of the Farallones. Water temperatures in the gulf were 0.5°C above the mean for May and June, 1989–97. Although temperatures were within the preferred range for chinook salmon in the ocean (Weatherley and Gill, 1995), altered oceanographic conditions may have changed the composition of the prey community, affecting the feeding of juveniles.

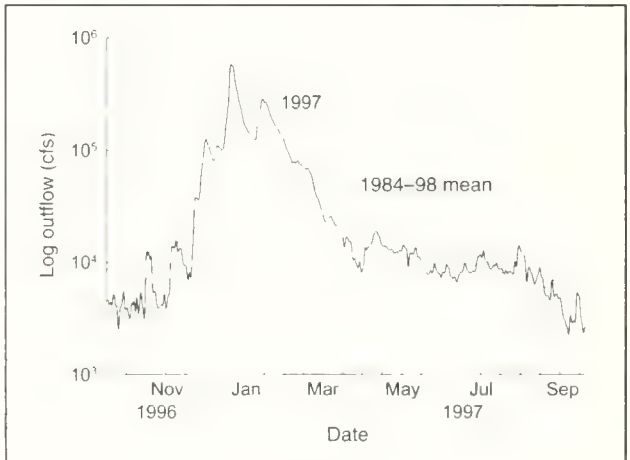

Figure 7

Freshwater outflow into the San Francisco Estuary from the Sacramento River–San Joaquin River Delta in 1997 compared with 1984–98 mean. Outflow data are mean daily cubic feet per second (cfs) from California Department of Water Resources, Sacramento, CA.

Among Pacific salmon, chinook salmon display the greatest variability of life history patterns, including time spent in fresh and brackish water before ocean entry, growth rates, the proportion maturing each year, and fecundity (Healey, 1991). Populations from the Central Valley of California are at the extreme southern end of the species' dis-

[3] Baylosis, J. I., J. L. Edmunds, J. L. Cole, and J. E. Cloern. 1998. Studies of the San Francisco Bay, California estuarine ecosystem: regional monitoring program results, 1997. U. S. Geological Survey Open-File Report 98-168, 194 p. [Available from U. S. Geological Survey, 345 Middlefield Road, Menlo Park, CA 94025.]

tribution and, like many populations at the edges of their distribution, may differ in their early life history from more centrally located stocks. Certainly, Central Valley chinook salmon are known to have unique characteristics such as unusually high fecundity, larger size at age (Healey, 1991), and large population size (PFMC[1]). Lesser estuarine dependence may be another unique trait of these southerly populations. Our data suggest that juvenile chinook salmon derive little benefit from their time spent in the San Francisco Estuary. There was little growth, depleted condition, and no accumulation of lipid energy reserves during the relatively limited time the fish spent transiting the 65-km length of the estuary. Extensive use of estuaries, especially by ocean-type chinook juveniles, seems more typical for populations to the north. Rearing and rapid growth have been characteristic of northerly stocks during extended periods of residence (Reimers, 1973; Healey, 1982; Simenstad et al., 1982; Pearcy, 1992) but were not evident in the San Francisco Estuary (Kjelson et al., 1982; our study).

Emigrating juvenile chinook salmon may not have always used the San Francisco Estuary as they do now. Extensive modification and degradation of the estuary by human activities in the past century or so may have altered the life history pattern of Central Valley chinook salmon populations. Loss of habitat, changes in prey communities, water-flow alterations and reductions, etc. may have contributed to less use of the estuary than previously.

Because Central Valley juvenile chinook salmon exhibit little estuarine dependence, they appear to benefit from expedited ocean entry. The rapid growth seen in the Gulf of the Farallones may confer potential for greater survival. Other chinook salmon studies have determined that larger juveniles are more likely to survive in the ocean (Higgs et al., 1992), leading to higher spawning returns (Burrows, 1969; Reimers, 1973). Faster growth and perhaps greater survival of juvenile chinook salmon, once in the ocean, may be a consequence of a typically favorable and stable thermal environment and the abundant food that results from the high biological productivity of this upwelling-dominated ecosystem (Ainley, 1990; McGowan et al., 1998). The abundant prey resources and lower metabolic costs associated with lower temperatures and ease of obtaining food may improve growth efficiency in the ocean compared with that in the San Francisco Estuary. Reliance on extended freshwater and estuarine residence prior to ocean entry could reduce Central Valley chinook salmon stocks, especially during prolonged periods of drought, which lower freshwater flows and raise temperatures. The ecological and evolutionary propensity of emigrating juveniles to conform to a strong ocean-type life history, with little estuarine dependency and a hastened ocean entry may be another unique attribute of Central Valley chinook salmon populations.

Acknowledgments

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Bottlenose dolphin (*Tursiops truncatus*) strandings in South Carolina, 1992–1996

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Abstract—From 1992 to 1996, 153 bottlenose dolphin stranded in South Carolina, accounting for 73% of all marine mammal strandings during this period. The objectives of our study were to evaluate data from these strandings to determine 1) annual trends in strandings, 2) seasonal and spatial distribution trends, 3) life history parameters such as sex ratio and age classes, 3) seasonal trends in reproduction, and 4) the extent to which humans have played a role in causing these strandings (human interactions). The results showed that 49% of the bottlenose dolphin strandings occurred between April and July; the greatest number of strandings occurred in July (n=22). There was a significant seasonal increase in the distribution of bottlenose dolphin strandings in the northern portion of the state from November to March. Bottlenose dolphin neonates stranded in every month of the year, except March and October, and represented 19.6% of the total number of strandings with known length (n=138). Fifty-five percent (n=15) of bottlenose dolphin neonatal strandings occurred between May and July. Bottlenose dolphins determined to have died as the result of human interaction accounted for 23.1% of the total number of bottlenose dolphin strandings (excluding those for which a determination could not be made). Incidents of bottlenose dolphin entanglements in nets accounted for 16 of these cases.

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When bottlenose dolphins (*Tursiops truncatus*) began stranding along the South Carolina coast during the 1987–88 die-off, state and federal authorities knew that it was an unusual mortality event. However, since there had been no organized marine mammal stranding network (MMSN) in the state (i.e. without standardized, historical data), the severity of the event could not be evaluated. To avoid this situation in the future, the National Marine Fisheries Service (NMFS) gave the South Carolina Department of Natural Resources (SCDNR) primary authority for the South Carolina Marine Mammal Stranding Network (SCMMSN) in January of 1991. An agreement between NMFS and SCDNR was entered into in 1992 under the Marine Mammal Protection Act (MMPA), and statewide, standardized stranding coverage was begun at that time.

In the epizootic event of 1987–88, it appeared that more than 50% of the migratory population of bottlenose dolphin perished along the eastern United States seaboard (Scott et al.[1]). As a result, the NMFS declared the coastal migratory stock of bottlenose dolphins depleted in 1993 (FR, 1993). Recommendations on data collection were set forth at the Atlantic Bottlenose Dolphin Workshop in Beaufort, North Carolina, 13–14 September 1993 (Wang et al., 1994) for the depleted coastal migratory stock of bottlenose dolphins. As a result, valuable life history data, tissue samples for histopathological and contaminant analyses, and seasonal stranding trends were obtained.

The objectives of this five-year study of stranded bottlenose dolphins in South Carolina were to determine 1) annual trends in strandings, 2) seasonal and spatial distribution trends, 3) life history parameters such as sex ratio and age classes, 3) seasonal trends in reproduction, and 4) the extent to which humans played a role in causing the strandings (human interactions). By examining the stranding data on a finer scale, we would be better prepared to evaluate any future unusual mortality event.

Methods

The South Carolina MMSN is composed of 20–25 people, including volunteers from the general public, university staff, federal, and state agency personnel. A separate group of the network, made up of SCDNR and NOS personnel and local veterinarians, respond to live stranded animals. A 1-800 telephone number, maintained by the SCDNR, receives reports from the public and transfers the information to the network volun-

[1] Scott, G. P., Burn, D. M., and L. J. Hansen. 1988. The dolphin die-off: long-term effects and recovery of the population. Proc. of the Oceans '88 Conf., NY, p. 819–823. Unpubl. manuscript. Southeast Fisheries Science Center, 75 Virginia Beach Dr., Miami, Florida 33149.

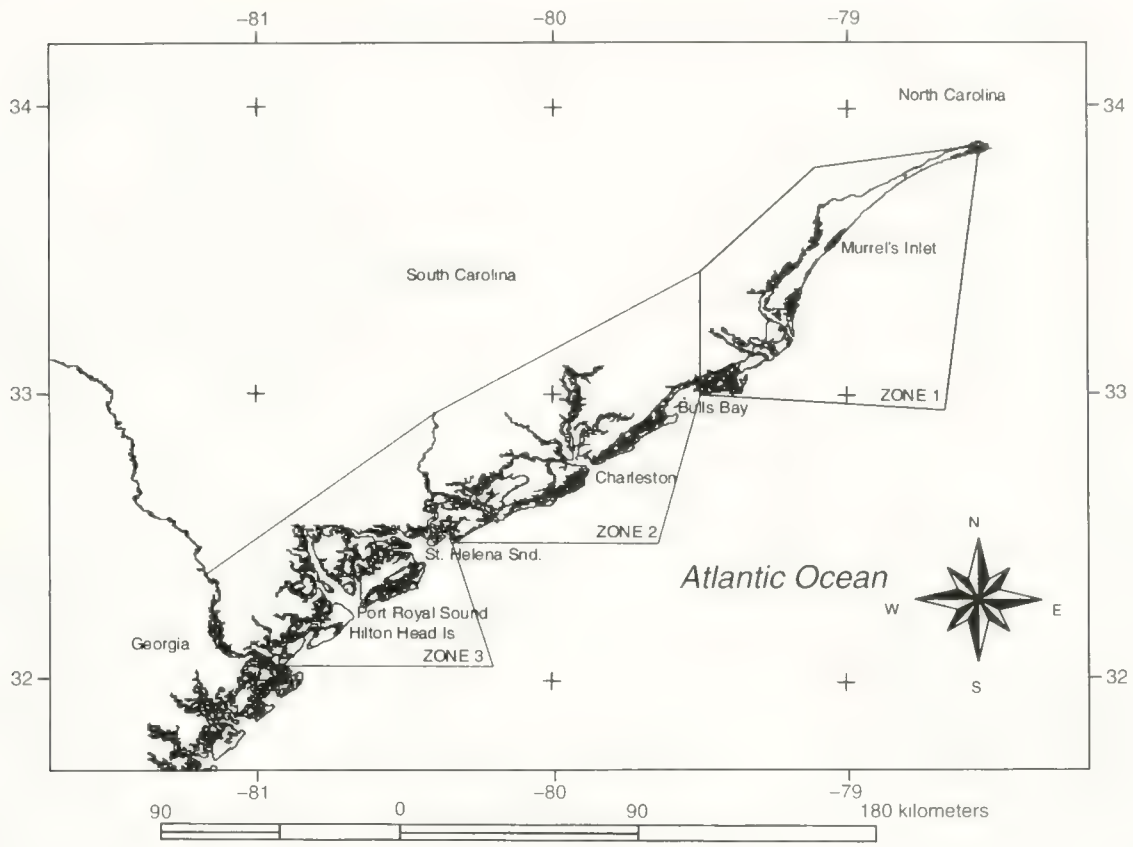

Figure 1

South Carolina coastline showing the three stranding zones: North Carolina border–Bulls Bay (zone 1), Bulls Bay–St. Helena Sound (zone 2), and St. Helena Sound–Georgia border (zone 3).

teers and the state coordinator. Since 1991, the SCDNR has flown the South Carolina coastline from Murrells Inlet to Port Royal Sound (approximately 200 km) once a month to look for stranded marine mammals on remote beaches (Fig. 1). These along-shore surveys were flown in a Cessna 180 high-wing SCDNR plane at 76 m altitude. Aerial reports were also received opportunistically from the U.S. Coast Guard, the Charleston County Sheriff's Department, and SCDNR, and reports were also received from SCDNR scientists (on the ground) who surveyed beaches for sea turtle nesting. Additional strandings were observed during aerial surveys of an investigation into dolphin mortality associated with a coastal shad-net fishery in 1995 (McFee et al., 1996).

For our study, the South Carolina coast was split into three geographical regions based on watersheds and hydrography (Brown, 1977): a northern zone (zone 1) from the North Carolina border to Bulls Bay (approximately 137 km), a central zone (zone 2) from Bulls Bay Island to St. Helena Sound (approximately 100 km), and a southern zone (zone 3) from St. Helena Sound to the Georgia border (approximately 75 km) (Fig. 1). Coverage of the coastline has been consistent since 1992. Although coverage on remote islands was lower in winter and higher in summer, it was constant from year to year. These areas are regularly patrolled by sea turtle personnel from the SCDNR and volunteers, many of whom are also members of the marine mammal stranding network.

Level A data (Hofman, 1991) were collected from each animal. Straight lengths of each bottlenose dolphin were obtained by measuring in centimeters (cm) from the tip of the upper jaw to the fluke notch. Photographs were taken for the majority of animals and were archived at the National Ocean Survey (NOS) Charleston Laboratory. Freshly dead animals were transported to the NOS Charleston Laboratory for necropsy or examined at the site of stranding according to NOS Charleston Laboratory protocol (Galloway and Colbert[2]). Animals in a moderate state of decomposition were not fully examined, but life history samples such as stomachs, ovaries, and skulls were collected. Necropsy reports were catalogued at the NOS Charleston Laboratory.

All stranded marine mammals that were accessible were examined for cause of death or evidence of human interaction (or for both). Stranding network volunteers and

[2] Galloway, S. B., and A. A. Colbert. 1997. Marine forensics manual. Part 1: marine mammals. Unpubl. manuscript. Center for Coastal Environmental Health and Biomoleculer Research, 219 Ft. Johnson Rd., Charleston, South Carolina 29412.

SCDNR personnel were trained to identify characteristic signs of human interaction, such as attached gear, rope or line marks, net marks, propeller cuts, straight-edge knife cuts, puncture wounds, etc. Animals with any of these characteristics were considered to be positive for human interaction. An assessment of stomach contents (full or empty), and histopathology (when available) to determine *ante-* or *post-mortem* injuries were used to corroborate findings. Photographs, and both necropsy and pathology reports from the United States Armed Forces Institute of Pathology (AFIP, Washington, D.C.) also were used to confirm these reports. Those animals that did not show any human interaction characteristics determined with photographs, necropsy, or AFIP pathology reports were considered to have no human interaction. For animals that were too decomposed, not fully examined, examined by untrained personnel, for whom there were inconclusive findings from necropsy or pathology reports, human interactions could not be determined. Therefore, each stranded bottlenose dolphin was classified into one of three categories to determine if human interaction was a possible cause, or contributing factor, in the death of the animals: 1) positive human interaction, 2) no human interaction, and 3) human interaction could not be determined (CBD).

Trends in the stranding data related to year, month, season, gender, and two specific age classes: neonate and females ≥220 cm, were investigated by using chi-square (χ^2) goodness-of-fit and analysis-of-variance (ANOVA) methods. A chi-square test for equal proportions was used to determine if there were differences in the number of strandings between years. An ANOVA was used to determine if there were differences in the number of strandings between months. To determine if there were seasonal trends in the strandings, the data were stratified into groups of three months representing four seasons: January–March (winter), April–June (spring), July–September (summer), and October–December (fall) (Fig. 2). Expected number of strandings for each season was determined by averaging over the 5-year period. To determine whether the stranding pattern for any given year deviated significantly from the "norm," we compared each year's seasonal number of strandings with the expected seasonal number by using a chi-square goodness-of-fit test. An ANOVA was performed to determine if there was a difference in the number of strandings between seasons. A chi-square goodness-of-fit test was used to determine seasonal trends between zones.

A chi-square goodness-of-fit test was used to determine if there was any difference in the proportion of male and female bottlenose dolphin strandings. A chi-square test for trend was used to test the hypothesis that there would be a downward trend in the number of animals that were of unknown sex due to increased training of stranding network volunteers in determining the sex of bottlenose dolphins. A chi-square goodness-of-fit test was used to determine if there was a difference in the number of strandings of females ≥220 cm between seasons.

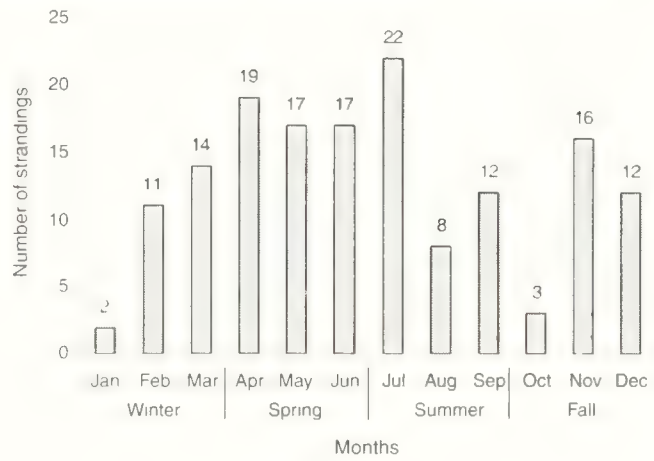

Figure 2

Number of bottlenose dolphin strandings in South Carolina for each month and season of the year from 1992 to 1996 (n=153). The numbers over each bar represent the number of strandings reported for that month.

Results

Yearly trends

From 1992 to 1996, 153 bottlenose dolphin strandings were reported along the coast of South Carolina. The number of strandings each year ranged from a low of 28 in 1992 to 33 in 1993 ($\bar{x}$=30.6) (Table 1); there was no significant difference among years (χ^2 test for equal proportions, P=0.968). Prior to 1992 the highest number of bottlenose dolphin reported stranded for one year was 17 in 1991 (the year the network was formed), excluding the unusual mortality event of 1987 (n=60).

Monthly trends

Over the five-year period, the greatest number of reports (22, or 14.4%) of bottlenose dolphin strandings occurred during July and the least in January (n=2) and October (n=3) (Fig. 2). There was no yearly differences in the total number of strandings by month from 1992 to 1996 (ANOVA, P=0.172).

Seasonal trends

The highest number of strandings occurred in spring (n=53, 34.6%) and the lowest number of strandings were recorded in winter (n=26, 17.0%). Strandings during the years 1992, 1994, 1995, and 1996 did not deviate from the expected pattern (χ^2 goodness-of-fit; P=0.994, 0452, 0.379, and 0.062, respectively), but the seasonal pattern in 1993 was significantly different (P=0.016). This was due in large part to the high number of strandings (n=14) in the fall, when we expected the number to be less than seven.

The ANOVA analysis indicated that the mean number of strandings differs significantly between seasons (P=0.021).

Table 1

Summary of results of human interaction from evaluations of bottlenose dolphins stranded in South Carolina from 1992 to 1996. "Gaff wounds" refer to puncture wounds made by the gaff, a long rigid pole with sharp point(s) used to spear fish or retrieve fishing gear.

	1992	1993	1994	1995	1996	Total
Total dolphins stranded	28	33	31	32	29	153
Human and fishery interactions						
Rope marks	2	0	0	3	4	9
Flukes cut off and mutilations	3	1	1	0	1	6
Boat strike	2	0	1	2	0	5
Blunt-object trauma	0	2	0	1	0	3
Net marks	0	0	0	0	1	1
Gaff wounds	0	1	0	0	0	1
Total	7	4	2	6	6	25
No human interaction	15	21	16	16	15	83
Human interaction could not be determined (CBD)	6	8	13	10	8	45
Percent of human or fishery interaction.[1]	31.8% (n=22)	16.0% (n=25)	11.1% (n=18)	23.1% (n=22)	28.6% (n=21)	27.3% (n=108)

[1] Calculated from total number of strandings minus CBD.

Given that 1993 was an unusual year in the stranding pattern, this year was excluded from the analysis. Specifically, the number of strandings was found to be higher in the spring than in other seasons (contrast analysis, P=0.012).

The majority of strandings occurred in the southern half of the state, zones 2 (n=67; 43.8%) and 3 (n=61; 39.9%). Seasonally, in zone 1 (n=25), 72.0% of its strandings occurred in fall and winter, whereas in zones 2 and 3, the majority of their strandings occurred in spring and summer, 68.7% and 70.5%, respectively. Seventy-three percent (n=11) of the bottlenose dolphins that stranded in the southern half of zone 1 did so between October to April. The difference in seasonal patterns of strandings between zones was significant (χ^2 goodness-of-fit; P=0.003).

Gender

The total number of stranded bottlenose dolphins with known sex was 115. The sex ratio for 1992–96 was 1.00:0.89, females (n=61) to males (n=54), not significantly different from parity (χ^2 test of association; P=0.979). A significant decrease in the proportion of unknown gender occurred during the period 1992–96 (χ^2 test for trend; P=0.012) because of an increase in the number of animals examined in necropsy.

Length classes

The total number of stranded bottlenose dolphins with known length was 138. Based on length-at-age data from known bottlenose dolphins (Read et al., 1993) and stranded bottlenose dolphin data from Texas (Fernandez and Hohn, 1998) the length data were stratified into five classes: class I (neonates—defined as a newborn having a folded dorsal fin or flukes or with umbilical remnants [or with both physical features]); class II (<184 cm, young of the year); class III (185–200 cm—calves); class IV (201–240 cm, mostly physically immature, especially females); and class V (>240 cm, mostly mature) (Fig. 3).

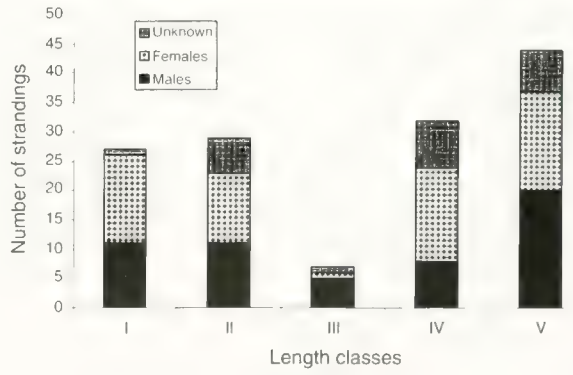

Figure 3

The number of strandings for males, females, and for bottlenose dolphin of unknown sex in each length-class stratum from 1992 to 1996 in South Carolina (class I=neonates; class II≤185 cm; class III=186–200 cm; class IV=201–240 cm; class V≥240 cm).

Males and females were distributed proportionately and evenly across the length classes with the exception of two classes: class III and class IV (Fig. 4). In class III, males

dominated (83.3%). Females were more prevalent in class IV (66.7%). Males showed the lowest numbers of strandings in class III (n=5) and highest numbers in class V (n=20).

Neonates Neonates represented 19.6% (n=27) of the total number (n=138) of strandings of dolphins with known length, ranging from 13.3% in 1993 to 24.1% in 1994 and were found in every month of the year, except March (Fig. 4). Twenty (74.1%) neonates stranded during the spring (n=14) and summer (n=6) months. June had the greatest number of strandings (n=7), followed by May (n=4) and November (n=4). Thirteen of the 27 neonates (48.1%) were <100 cm. Twelve of these stranded during the spring and fall months. More female neonates (1.3:1.0) stranded in South Carolina than males, though this difference was not significant (χ^2 test of association; P=781).

Twenty-four (88.9%) of the neonates stranded in zones 2 (n=13) and 3 (n=11). Neonates were found dead in the inner waterways (n=18) and along the outer beaches (n=9). Twelve of the dead neonates found in the inner waterways were retrieved while they were floating.

Females ≥220 cm Females found at a length that showed them capable of being reproductively mature (i.e. ≥220 cm) (Odell, 1975; Mead and Potter, 1990) represented approximately 50% (n=30) of the total number (n=61) of females stranded. The proportions of females ≥220 cm stranded each year were similar, with the exception of those for 1992, where only one out of seven females was this length. However, this finding may be biased, except for 1994, because of the number of animals ≥220 cm that were of unknown sex. The proportion of strandings of females ≥220 cm in each season was statistically significant (χ^2 goodness-of-fit; P=0.011). A large proportion of the lengths of female bottlenose dolphin stranded during winter (40%) and spring (40%) were ≥220 cm compared with lengths for summer (6.7%) and fall (13.3%).

Human interaction

The total number of stranded bottlenose dolphins where either human interaction or no human interaction could be determined was 108. Twenty-five bottlenose dolphin strandings, averaging five per year, showed evidence of human interaction. Eighty-three showed no signs of human interaction and 45 could not be determined (Table 1). Incidents of net entanglements, made evident by rope or line marks, net (mesh) marks, and mutilations, accounted for 16 of the human interaction cases. Incidence of confirmed human interaction on bottlenose dolphins was highest from March to July (n=18). Rope or line marks were more prevalent from February through May (n=8). The ratio of males (n=10) to females (n=11) was 1:1 in the number of positive human interactions, but there were differences in the length class and types of interaction between the sexes. Of the five males that were involved with net entanglements, four were less than 218 cm. Of the eight females associated with entanglements, seven were greater than 210 cm and six of these were >220 cm. Eighty-eight percent

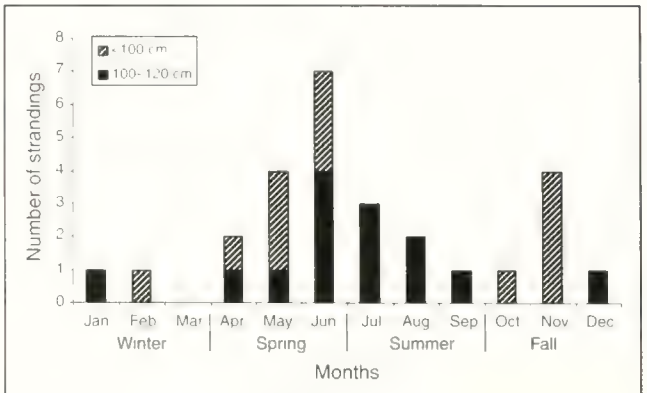

Figure 4

Total number of strandings of neonatal bottlenose dolphins in each month from1992 to1996 (n=27). Diagonally lined boxes represent those neonates <100 cm in length.

of reported human interactions occurred in zones 2 (n=10) and 3 (n=12). Preliminary analysis of stomach contents from bottlenose dolphins stranded on account of human interaction in our study showed that the majority of animals had full stomachs with shrimp or fish remains (or both) (McFee, personal obs.).

Discussion

Despite the establishment of an organized marine mammal stranding network in the southeastern United States since 1990, there has been little published on basic data from stranded bottlenose dolphins other than from reports that can be found as "gray literature." Results from our study indicated the value of analyses of strandings and produced three main findings: 1) the northern portion (zone 1) of the state reported significantly more bottlenose dolphin strandings between November and March 2) neonatal bottlenose dolphin strandings occurred with more frequency between May and July and 3) evidence of human interaction as the cause, or contributing factor, in the deaths of some bottlenose dolphins.

Several hypotheses regarding stock structure of Atlantic bottlenose dolphins have been proposed (Hohn, 1997). One hypothesis is that a single coastal migratory stock migrates seasonally from Long Island, New York, to the central east coast of Florida (Scott et al[3]). The other hypothesis is that multiple bottlenose dolphin stocks exist that include 1) year-round residents with small home ranges, 2) seasonal residents with large home ranges, or 3) migratory groups with long-range movements (Hohn, 1997).

Bottlenose dolphins begin to leave Virginia in mid-October and are mostly absent by mid-November (Swingle,

[3] Scott, G. P., D. M. Burn, and L. J. Hansen. 1988. The dolphin die-off: long-term effects and recovery of the population. Proc. of the Oceans '88 Conf., NY, p. 819–823. Unpubl. manuscript. Southeast Fisheries Science Center, 75 Virginia Beach Dr., Miami, Florida 33149.

1994; Barco et al., 1999). At about the same time, large numbers of dolphins begin to appear along the "Grand Strand" in northern South Carolina (zone 1) in October and peak in early November, according to bottlenose dolphin sighting data collected during photo-identification studies (Young[4]). During the 1987 bottlenose dolphin die-off, 52 bottlenose dolphin strandings were reported in South Carolina from October through December (Wang et al., 1994). Densities of bottlenose dolphins during a one-year aerial survey of waters from the shore to the Gulf Stream showed the greatest numbers of sightings in fall 1982 (concentrated in the Carolinas), and in winter 1983 (concentrated in northern Florida) (Wang et al., 1994).

Stranding patterns may reflect the abundance of animals. Although large numbers of dolphins occur year-round in South Carolina, there appears to be a peak in strandings in the late fall (November) which would coincide with data from Myrtle Beach (Young[4]), Charleston (Zolman, 1996), and Hilton Head Island (Petricig, 1994) in which greatest abundance of dolphins occurred in late fall. Water temperature, distribution of prey, and use of coastal shrimp trawlers have been implicated as reasons for dolphin movements and abundance in certain areas (Kenney, 1990; Mead and Potter, 1990; Bräger et al., 1994; Fertl, 1994). The late fall increase in the number of strandings in South Carolina could be due to the increased numbers of dolphins from any one of the migratory stocks suggested in the above hypotheses. Zone 1, in particular, provided evidence that a portion of the strandings is from a coastal bottlenose dolphin migratory stock or stocks. The northern half of zone 1 is known as the "Grand Strand" which extends from N. Myrtle Beach to Murrells Inlet (approximately 59 km). This area is highly populated and animals coming ashore here are found and reported regardless of the season of the year. Coverage in the southern half of zone 1 (approximately 78 km) tends to be high from May to September when the beaches are monitored for sea turtle nesting and hatching, but low during October to April. However, the majority of strandings occurred during the latter time period. This may suggest an influx of bottlenose dolphins migrating through zone 1 from October to April, either from the north or south.

We would expect bottlenose dolphin mortality to be similar to that for terrestrial mammals (Ralls et al., 1980): high neonatal and first-year mortality and high adult mortality, and an even distribution of mortality among males and females. If stranding data reflect natural mortality patterns, our results and other studies (Hersh and Duffield, 1990; Hersh et al., 1990; Wells and Scott, 1990; Fernandez and Hohn, 1998) are consistent with mortality patterns suggested for terrestrial mammals. Further, the percentage of stranded bottlenose dolphin neonates (19.6%) was intermediate when compared with that of previous studies (observations in Sarasota, Florida, 36.8% [Wells and Scott, 1990], and Indian/Banana River System, Florida, 11.2% [Hersh et al, 1990]), but similar to that of Texas (20.0% [Fernandez and Hohn, 1998]). We can only assume that mortality during the first year of life is high for bottlenose dolphins regardless of geographical location.

Age and ovarian analysis of stranded bottlenose dolphins ≥220 cm (Odell, 1975; Mead and Potter, 1990) are necessary to determine whether these animals are sexually mature and whether the seasonal patterns noted above correlated with a seasonal reproductive cycle. Seasonal reproduction cycles are complex and not well studied in the South Carolina bottlenose dolphin population but have been demonstrated where adaptations to local environmental conditions may influence seasonal reproductive cycles (Urian et al., 1996).

Over large geographic regions, bottlenose dolphins exhibit year-round calving cycles, but within small geographic regions there may be a higher degree of local reproductive seasonality (Urian et al., 1996). A unimodal seasonal distribution of neonate bottlenose dolphin strandings was noted from Sarasota, Florida, and along the Texas coast, although peak neonatal strandings occurred in different months of the year—May and March, respectively (Urian et al., 1996; Fernandez and Hohn, 1998). A bimodal seasonal distribution was noted for the east coast of Florida in the Indian River Lagoon (Urian et al., 1996). In Sarasota, Florida births have been noted in every month of the year (Urian et al., 1996). Although sample size over the five-year period for our study was too small to estimate significance of trends, our results showed a unimodal distribution and a peak number in June. However, more data may show a bimodal distribution of bottlenose dolphin neonatal strandings because of a second peak that occurred in November. These peaks do not appear to be a function of effort because the majority of neonate strandings occurred on the banks of inland waterways or the neonates were found as floating bodies. The number of neonates in the Stono River estuary, Charleston, South Carolina, peaked in the fall, during a 15-month photo-identification study (Zolman, 1996). Further, all four neonate bottlenose dolphins stranded in South Carolina in November were <100 cm; therefore these animals may have been aborted near-term fetuses.

The determination of human interaction as the cause of mortality for bottlenose dolphins is an important role of the marine mammal stranding networks and can influence management decisions. For example, the Marine Mammal Protection Act (MMPA), as amended in 1994, required that annual stock assessment reports for each stock of marine mammals be prepared. One of the items to be addressed in these reports was a description of commercial fisheries that interact with each stock and the level of mortality caused on each stock by each fishery (Waring et al., 1999). The level of mortality each fishery contributes to a stock, in turn, is essential in determining potential biological removal (PBR) estimates for the stock and the subsequent classification category that regulates each fishery (Waring et al., 1999). The current PBR for Atlantic coastal bottlenose dolphins is 25 (Waring et al., 1999). In a study on the American shad (*Alosa sapidissima*) fishery in South Carolina from 1994 to 1995, no human interactions were shown to be a cause of bottlenose dolphin mortality in the area of fishery effort (McFee et

[4] Young, R. 1998. Personal commun. Coastal Carolina University, P.O. Box 1954, Conway, SC 29526.

al., 1996). As a result, the South Carolina shad fishery retained its original classification as a category-III fishery (i.e.unlikely to take marine mammals in the course of operation) as described in the MMPA amendments of 1988.

Bottlenose dolphin mortality due to human interactions is variable along the eastern United States and Gulf of Mexico (Wang et al., 1994). Incidents of human interaction in South Carolina were also variable over our five-year study period. We believe that the number of bottlenose dolphins in our study showing positive human interaction is a minimum because determination of human interaction cases is difficult to assess owing to a lack of trained personnel, the decomposition of some carcasses, and the presumption that some interactions do not leave any physical evidence. It was a rare occurrence to have gear attached to the carcass; therefore, determination of human interaction was usually made by observing external marks such as cross-hatched lines or lines imprinted by the fishing gear. Human interaction as a cause or contributing factor in a dolphin's death can include fishery interactions (crab pots, trawls, etc.), boat collisions, gun shot wounds, environmental contaminants (agricultural run-off, pesticide use, oil spills). These interactions can result in acute (drowning in a net) or chronic (environmental contaminants) death, show physical evidence (net marks) on the body or none at all.

The percentage of human interaction cases observed in South Carolina was low compared with those in North Carolina strandings (>35% in some years; Wang et al., 1994; FR, 1997). Resident bottlenose dolphins in South Carolina appear to be exposed to different fishing operations than do bottlenose dolphins that migrate through or inhabit North Carolina waters. Net marks were the most common observation (10.5 animals per year) of human interaction cases in North Carolina (FR, 1997), whereas in South Carolina only one presumed net-caught animal was observed over a five-year period. In South Carolina incidents of entanglements as evidenced by rope or line marks are puzzling. At this time, it is highly speculative as to which fishery in South Carolina may be responsible for the incidence of entanglements associated with rope or line marks.

There is evidence to suggest that relationships exist between gender and lengths of various species of cetaceans involved with human interaction (Perrin et al., 1994; Cox et al., 1998). In our study small male bottlenose dolphins and female bottlenose dolphins ≥220 cm showed evidence that they were subject to human interaction. One study found that females with calves spent more time feeding at shrimp boats than did lone animals (Fertl, 1994). Food intake for lactating females can increase dramatically (Cockroft and Ross, 1990). Although heavy-feeding behavior may be energetically beneficial, it may also be costly to both the calf and mother by exposing them to fishing gear and predation.

In summary, the stranding data collected for bottlenose dolphins in South Carolina from 1992 to 1996 provides baseline information for the demographics, life history studies, and management concerns for comparing future stranding rates of bottlenose dolphins in South Carolina. Although it cannot be definitively stated that stranding rates coincide with a portion of a migratory stock, strandings in the northern portion (zone 1) do increase during a period of greater dolphin abundance. More years of data will further elucidate the seasonal reproduction distribution for bottlenose dolphin. Finally, the detection of human interaction as a cause or contributing factor in the deaths of some bottlenose dolphins in South Carolina has demonstrated the need to continue the effort to report these incidents for management purposes.

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Validated age and growth of the porbeagle shark (*Lamna nasus*) in the western North Atlantic Ocean

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Abstract—Growth parameters were estimated for porbeagle shark (*Lamna nasus*) in the northwest Atlantic Ocean on the basis of vertebral annuli. A total of 578 vertebrae was analyzed. Annuli were validated up to an age of 11 years by using vertebrae from recaptured oxytetracycline-injected and known-age sharks. Males and females grew at similar rates until the size of male sexual maturity, after which the relative growth of the males declined. The growth rate of the females declined in a similar manner at the onset of maturity. Growth curves were consistent with those derived from tag-recapture analyses (GROTAG) of 76 recaptured fish and those based on length-frequency methods with measurements from 13,589 individuals. Von Bertalanffy growth curve parameters (combined sexes) were L_∞ = 289.4 cm fork length, K = 0.07 and t_0 = –6.06. Maximum age, based on vertebral band pair counts, was 25 and 24 years for males and females, respectively. Longevity calculations, however, indicated a maximum age of 45 to 46 years in an unfished population.

The porbeagle (*Lamna nasus*) is a large pelagic shark in the family Lamnidae that occurs in the cold, temperate waters of the North Atlantic, South Atlantic, and South Pacific oceans. The species extends from Newfoundland to New Jersey in the western North Atlantic (Castro, 1983), and from Iceland and the western Barents Sea to Morocco and the Mediterranean in the eastern North Atlantic (Compagno, 1984). Directed commercial fisheries for porbeagle have existed in the western North Atlantic in both U.S. and Canadian waters since the early 1960s (Campana et al.[1]). The fishery collapsed in 1967, apparently from overfishing. Canadian fishermen maintained low and apparently sustainable catches in the 1970s and 1980s, which allowed the stock to rebuild. A renewed fishery for porbeagle began in both the United States and Canada in the 1990s (Campana et al.[1]).

Accurate age determinations are necessary for both the assessment and management of the porbeagle shark because they form the basis for calculations of growth and mortality rates, age at maturity, age at recruitment, and estimates of longevity. Aasen (1963), in an early study of porbeagle growth, generated a growth curve for the western North Atlantic population based on analyses of length frequencies from a single year and on vertebral readings of one fish. However, he did not provide any independent confirmation of the accuracy of his age estimates. Francis and Stevens (2000) used length-frequency analysis to estimate the growth of juvenile porbeagles in the South Pacific. Both of these studies indicated that porbeagle grow relatively rapidly through the first year of life, but only minimal information has been available for older fish.

In view of the history of the porbeagle fishery and the need for accurate biological information for management of this species, an intensive U.S.-Canadian cooperative research program was initiated in 1999 to obtain detailed life-history and population data. This study reports on one portion of this program, specifically, the use of vertebrae to determine age and growth. The vertebral growth readings were validated as annuli on the basis of recaptures of tetracycline-injected and known-age sharks and verified by comparison with growth curves based on tag-recapture and length-frequency analyses.

[1] Campana, S., W. Joyce, L. Marks, P. Hurley, L. J. Natanson, N. E. Kohler, C. F. Jensen, J. J. Mello, and H. L. Pratt Jr. 2000. The rise and fall (again) of the porbeagle shark population in the Northwest Atlantic. Unpubl. manuscr. Marine Fish Division, Bedford Institute of Oceanography, P.O. Box 1006, Dartmouth, Nova Scotia, Canada B2Y 4A2.

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Materials and methods

Vertebral aging

Vertebral samples from porbeagle sharks were obtained between 1966 and 1999 on board commercial and research vessels. The majority of samples (97%) were collected after 1990 on Canadian commercial longline vessels. Sampling took place in U.S. and Canadian waters between Massachusetts (NE U.S.) and the Grand Banks (off southern Newfoundland) and all individuals were treated as belonging to the same stock on the basis of tagging data (Campana et al.[2]). Multiple vertebrae were removed from the area just above the branchial chamber wherever possible; except on commercial vessels where samples were obtained closer to the head. Vertebrae were then stored frozen or in 70% ETOH until processing.

Only samples that had measured fork length (FL—tip of the snout to the fork in the tail, over the body) or total length (TL—tip of the snout to a point on the horizontal axis intersecting a perpendicular line extending downward from the tip of the upper caudal lobe to form a right angle, over the body; Kohler et al., 1995) were used. All lengths reported in this document are over-the-body FL unless otherwise noted. Total length in centimeters (cm) can be converted to FL cm by using the regression equation (Campana et al.[1]):

$$FL = 0.885(TL) + 0.99 \qquad [n = 361\ r^2 = 0.99].$$

One vertebra from each sample was removed for processing. The centrum was sectioned by using a Ray Tech Gem saw with two diamond blades separated by a 0.6-mm spacer. Each centrum was cut through the middle along the sagittal plane and the resulting "bow-tie" sections were stored individually in capsules in 70% ETOH. Each section was digitally photographed with a MTI CCD 72 video camera attached to a SZX9 Olympus stereo microscope by using reflected light. Magnification depended on the size of the section and varied from 4× to 12.5×. Band pairs (consisting of one opaque and one translucent band) were counted and measured from the images by using Image Pro 4 software (Media Cybernetics, 1998). Measurements were made from the midpoint of the isthmus of the full bow-tie to the middle of the opaque growth bands at points along the internal edge of the corpus calcareum (Fig. 1). The vertebral radius (VR) of each centrum was measured from the midpoint of the isthmus to the distal margin of the intermedialia along the same diagonal as the band measurements.

The identity of the birth band in the vertebra was confirmed through comparison of the birth band radius (BR) measurements to vertebral radius measurements of late-term embryos, early young-of-the-year, and late age-0 fish. The late-term embryo vertebral samples were obtained from the South Pacific porbeagle population, courtesy of Malcolm Francis.[3] The assumptions were made that vertebral growth *in utero* was comparable between the two populations and that measurements of the rehydrated dried South Pacific vertebrae were similar to those from wet NW Atlantic preparations.

The relationship between VR and FL was calculated in order to confirm the interpretation of the birth band and to determine the best method for back-calculation of size-at-age data. The FL to VR relationship was curvilinear; therefore, the data were ln-transformed before linear regression. The Fraser-Lee equation of the ln-transformed data was derived for back calculation:

$$\frac{\ln(FL_a) = b + (\ln|FL_c| \quad b)(\ln radius_a)}{(\ln radius_c)}$$

where a = age;
b = intercept from the FL-VR regression; and
c = capture.

Validation

The accuracy of the vertebral band pair counts as annual indicators was determined by using both known-age recaptures and recaptures of oxytetracycline (OTC)-injected and tagged individuals. Vertebrae from young of the year (YOY) sharks whose FL was measured at both tagging and recapture were used for known-age analyses. Band pair counts were compared with time at liberty to determine band pair periodicity. One hundred and fifty-five porbeagles of various lengths were also tagged and injected with 25 mg/kg of OTC (senior author, unpubl. data) Returned vertebrae from these sharks were examined with reflected UV light for the OTC mark. The number of band pairs distal to the OTC mark were then compared with the number of years at liberty.

Data analysis

Aging bias and precision of annulus counts were examined by using age-bias plots and the coefficient of variation (Campana et al., 1995). Two readers independently counted 100 vertebral sections from which the pair-wise age-reader comparisons were generated.

Von Bertalanffy growth functions (VBGF) were fitted to the length-at-age data by using the following equation (von Bertalanffy, 1938):

$$L_t = L_\infty (1 \quad e^{-K(t \quad t_0)}),$$

where L_t = predicted length (cm) at age t;
L_∞ = mean theoretical maximum fork length;
K = a growth rate parameter (per yr); and
t_0 = the theoretical age (yr) at zero length.

[2] Campana, S., L. Marks, W. Joyce, P. Hurley, M. Showell, D. Kulka. 1999. An analytical assessment of the porbeagle shark (*Lamna nasus*) population in the northwest Atlantic. Canadian Stock Assessment Secretariat Research Document 99/158, 57 p. Marine Fish Division, Bedford Institute of Oceanography, P.O. Box 1006, Dartmouth, Nova Scotia, Canada B2Y 4A2.

[3] Francis, M. 2000. Personal commun. National Institute of Water and Atmospheric Research P.O. Box 14-901, Wellington, New Zealand.

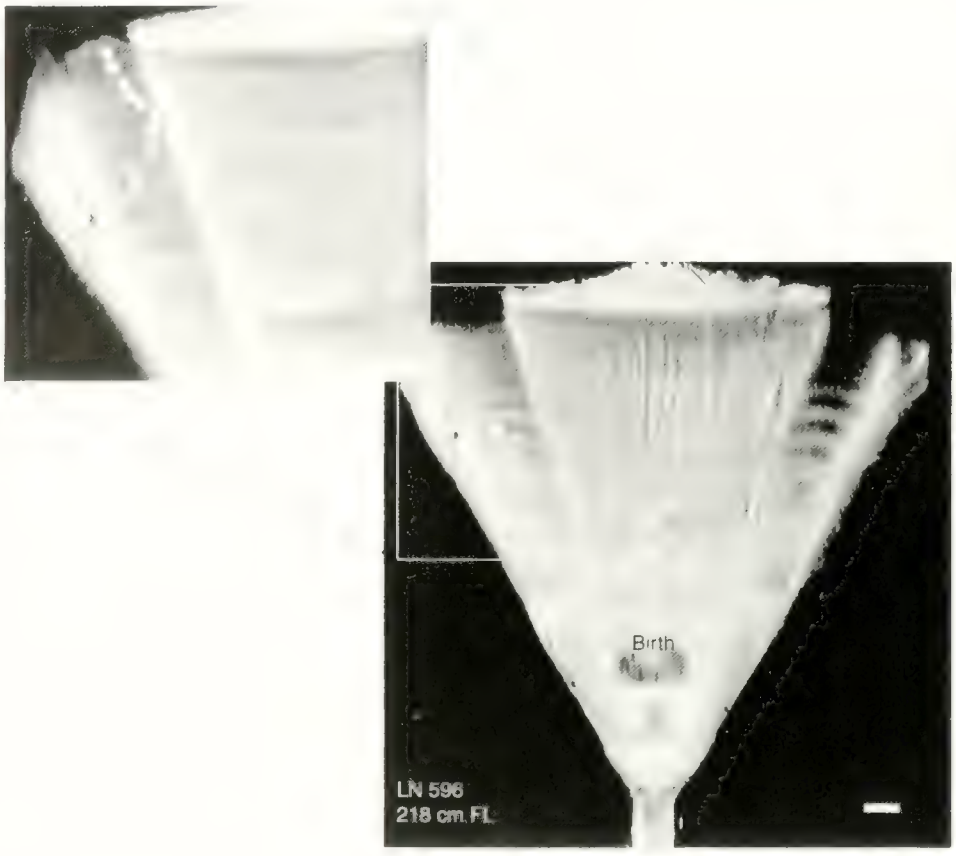

Figure 1

Photograph of a vertebral section from a porbeagle estimated to be 15^{+} years old. Insert shows higher magnification view of narrow bands at edge. Scale bar = 1 mm. White dots are on annuli.

The VBGF was calculated by using the nonlinear regression function in Statgraphics. Locally weighted least squares regression (LOESS) curves were fitted to the FL vs. age data for each sex by using Statgraphics (Manguistics, 1997).

Length frequency

Length-frequency data were obtained from the Canadian International Observer Program operating primarily on the Scotian Shelf, and some data from the Grand Banks. Although the entire data set (1986–98) was analyzed, only data from the most complete year (1991) were used for the final analysis.

Monthly length-frequency histograms were developed for eight months of 1991 for modal analysis. Calculations of mean fork length and annual growth rate for ages 0 and 1 were based on the first two modes of these data, which were easily distinguished and tracked across months.

MULTIFAN (Fournier et al., 1990) was used to estimate the VBGF parameters from the 1991 length-frequency data. The model analyzes multiple length-frequency distributions by using a maximum likelihood method to estimate the number of age classes present and VBGF parameters L_{∞} and K. An initial systematic search was conducted based on user-supplied K values and age classes. Constraints were placed on the estimates of length at age for the first two age classes. MULTIFAN allows the user to start with a generalized search and then add parameters to further refine the model. The initial search included estimates of K ranging from 0.05 to 0.25 and age classes of 11 through 20. The hypotheses tested were the following: 1) constant length standard deviation for all age classes; 2) variable length standard deviation for all age classes; 3) constant length standard deviation for all age classes with seasonal growth; and 4) variable length standard deviation for all age classes with seasonal growth. A model incorporating constant length standard deviation was fitted first with the additional parameters added sequentially. Results from the four models were compared by using log-likelihood tests following Fournier et al. (1990) and Francis et al. (1999).

The von Bertalanffy growth parameter t_0 was estimated from the equation

$$t_0 = t_1 - a_1, \quad (1)$$

where a_1 = the age estimated by MULTIFAN for the youngest age class at the time it first appeared in the length-frequency samples; and
t_1 = the time elapsed in years between the theoretical birthday and the first appearance of the youngest year class in the samples.

The theoretical birthday was defined as 1 April based on the gestation period and the time of mating (Jensen et al.[4]). The first appearance of the youngest age class in the samples was 1 July.

The model with seasonal growth components required the use of a modified von Bertalanffy equation to incorporate the amplitude and phase of the seasonal growth:

$$L_t = L_\infty\left(1 - e^{-\{K[t - t_0 + (\phi/2\pi)\sin[2\pi((12t+1)/12) - \phi_2]]\}}\right), \quad (2)$$

where ϕ_1 = amplitude; and
ϕ_2 = (MULTIFAN phase) + t_1 (from Eq. 1).

Tag-Recapture analysis

Data from three independent tagging studies from the western North Atlantic Ocean were combined for tag and recapture analysis. In the 1960s, 542 porbeagles were tagged and 53 recaptured as part of a Norwegian study of the unfished population. In 1994 through 1996, the Canadian Department of Fisheries and Oceans (DFO) conducted a tagging program in which 256 porbeagles were tagged and 25 recaptured. Between 1979 and 1999, members of the National Marine Fisheries Service's (NMFS) Cooperative Shark Tagging Program tagged 1034 and recaptured 119 porbeagles. Sharks were tagged and recaptured by biologists and commercial and recreational fishermen in the United States and Canada and by biologists in the Norwegian study. All measurements were converted to FL by using the morphometric conversions reported in Campana.[1] Where Norwegian measurements were reported as Aasen's (1963) total length, they were converted to FL with the equation:

$$FL = 0.93TL.$$

Only those sharks reliably measured at the time of tagging and recapture were used in the analyses. Reliability was based on prior knowledge of the individual's expertise in measuring the shark or on detailed questioning of those individuals as to the method used. The majority of sharks were measured by NMFS biologists or their representatives.

The Gulland and Holt (1959) and Francis (1988a) models were used to generate VBGFs from the tag-recapture data. The Gulland and Holt (1959) method uses graphical interpretation of the recapture data to produce estimates of L_∞ and K. Specifically, annual growth rate (cm/yr) was plotted against average FL (cm) between tagging and recapture to calculate linear regression coefficients. The slope of the line is equal to $-K$ and the x-axis intercept is equal to L_∞.

The Francis (1988a) method (GROTAG) uses maximum likelihood techniques to estimate growth parameters and variability from tagging data. With this method, a coefficient of variation of growth variability (v), the mean and standard deviation of measurement errors (m and s), and outlier contamination (p), are estimated as well as growth rates at two user-selected lengths (α and β). The reference lengths, α and β, were chosen to lie within the range of tagged individuals. The form of the von Bertalanffy equation becomes

$$\Delta L = \left[\frac{\beta g_\alpha - \alpha g_\beta}{g_\alpha - g_\beta} - L_1\right]\left[1 - \left(1 + \frac{g_\alpha - g_\beta}{\alpha - \beta}\right)^{\Delta T}\right], \quad (3)$$

where L_1 = length at tagging;
ΔL and ΔT = increments in length and time, respecitively; and
g_α and g_β = mean annual growth rates at the arbitrary lengths α and β.

The simplest model, with minimal parameters (α and β), was used initially with additional parameters added to successively increase model complexity. Significant improvement in the model results were determined by using log likelihood ratio tests (Francis, 1988a). The modeling was carried out by using a Solver-based spreadsheet in MS Excel (Simpfendorfer[5]).

The value of t_0 cannot be estimated from tagging data alone; rather it requires an estimate of absolute size at age, such as size at birth, and was calculated with the VBGF by solving for t_0 such that

$$t_0 = t + (1/K)\left[\ln\{(L_\infty - L_t)/L_\infty\}\right], \quad (4)$$

where L_t = known length at age (size at birth);

The t_0 values were calculated from an average size at birth of 67 FL cm (Aasen, 1963) with $t = 0$.

Longevity

Several methods were used to estimate longevity. The oldest fish aged from the vertebral method provides an initial value, but is likely to be underestimated in a fished population. Taylor (1958) defined the life span of a teleost species as the time required to attain 95% of

[4] Jensen, C., L. J. Natanson, H. L. Pratt Jr., N. E. Kohler, and S. Campana. 2001. The reproductive biology of the porbeagle shark, *Lamna nasus*, in the western North Atlantic Ocean. Unpubl. manuscript. Apex Predators Program, NMFS, 28 Tarzwell Dr., Narragansett, RI 02882.

[5] Simpfendorfer, C. 2000. Unpubl. data. Mote Marine Laboratory, 1600 City Island Park, Sarasota, FL 33577.

the L_∞. Using a wide range of species, Hoenig (1983) calculated the relationship between longevity, t_{max}, and the natural mortality rate, M, needed to attain one percent of initial abundance in an unfished population as

$$\ln(M) = 1.44 - 0.982 \ln(t_{max}).$$

However, a relationship based on other species need not be used (Campana et al.[2]). Assuming a constant instantaneous natural mortality, M, in an unfished population, the following equation applies:

$$\text{Ln (proportion of fish that survive to age } t_{max}) = -Mt_{max}.$$

As with Hoenig (1983), this equation was evaluated at a value of 0.01 for the proportion of fish that survive.

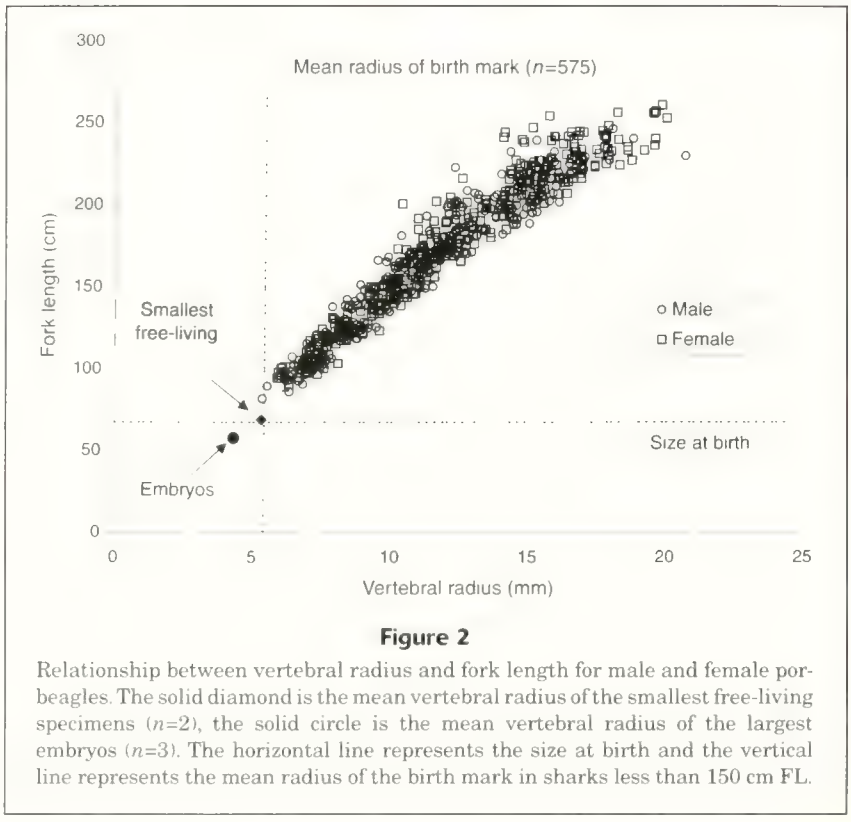

Figure 2

Relationship between vertebral radius and fork length for male and female porbeagles. The solid diamond is the mean vertebral radius of the smallest free-living specimens (n=2), the solid circle is the mean vertebral radius of the largest embryos (n=3). The horizontal line represents the size at birth and the vertical line represents the mean radius of the birth mark in sharks less than 150 cm FL.

Results

Vertebral aging

Vertebral samples from 578 porbeagles were used in our analysis; 283 were males, 292 were females, and 3 were of unknown sex. All vertebrae had distinct band-pair patterns (Fig. 1). The birth mark was indicated by a slight change in angle of the centra and was often the most pronounced first band pair. Subsequent annuli consisted of a pair of alternating opaque and translucent bands that crossed the entire centrum, except in the oldest sharks. Band-pair width decreased with age, narrowing substantially in the oldest individuals (Fig.1).

The FL-VR relationship was curvilinear (Fig. 2), and although the ln-transformed relationship was not completely linear, it was preferable. Therefore, regressions were calculated based on the ln(FL)-ln(VR) relationship where

$$\ln(\text{FL}) = 0.88 \times \ln(\text{VR}) + 2.96 \qquad [r^2=0.94, n=575].$$

There was no significant difference between the regressions of males and females (ANCOVA, P>0.01).

The identity and location of the birth band was confirmed through comparison of the BR of all individuals to the VR of YOY and embryos. The mean VR of three late-term embryos ranging in size from 56.1 to 58 cm FL (mean VR=4.3 mm, CI=0.57) was slightly less than the mean BR value of the total sample (mean BR=5.4 mm, CI=0.03 mm, n=578). The mean BR those of two early YOY (67.7 and 69.2 cm FL) were also similar to those of the total sample (mean VR=5.3 mm, CI=1.27 mm). The VR of the age-0 individuals ranging in size from 76.5 to 100 cm FL (mean VR=6.2 mm, CI=0.31 mm, n=16) was slightly higher (Fig. 2). The placement of the mean BR between the VR of both the YOY and embryos indicates that the birth ring was identified correctly. The birth ring radius increased slightly with increasing FL likely because of an increase in the length of the isthmus of the bow-tie section in larger sharks.

Validation

Known-age recaptured porbeagles and OTC-injected recaptured porbeagles returned with vertebrae confirmed the accuracy of the band-pair counts as indicators of age. Six porbeagles tagged as YOY were recaptured after three to five years at liberty (Table 1). Of the four sharks that were recaptured in the spring, all had translucent material at their growing edge. In contrast, the two sharks recaptured in November had a broad opaque zone at the growing edge. In each case, the vertebral band-pair counts matched the expected counts based on time at liberty (Fig. 3). Vertebrae from six OTC-injected sharks were returned after 0.02 to 2.5 years at liberty. All vertebrae showed a distinct fluorescent mark indicating that the OTC was incorporated within six days (0.02 years) of injection (Fig. 3). Two of the OTC-injected sharks were at liberty for over one year and were used for validation. In both cases, the expected number of growth bands was deposited on the vertebrae between the date of injection and the date of recapture (Table 1). The shark at liberty for 2.5 years had 3 full bands after the OTC mark, the last band having formed just prior to capture. The OTC-injected shark at liberty for 1.5 years was an adult (189.8 cm FL) at tagging and was aged, by vertebrae, to be 11 years at recapture. This

Table 1

Tag-recapture data for the OTC-injected and known-age recaptured porbeagles with vertebrae. TFL = fork length at tagging, RFL = fork length at recapture.

	Sample number	Sex	TFL (cm)	RFL (cm)	Date tagged	Date recaptured	Years at liberty	Growth (cm)	No. of bands past birth mark
Known age	LN 207	F	104.0	178.0	10 Nov 1993	23 Apr 1999	5.4	74.0	6
	553	M	85.0	160.0	1 Nov 1994	9 Nov 1999	5.2	75.0	5
	206	M	100.0	153.0	24 Oct 1994	27 May 1999	4.6	53.0	4
	556	F	97.0	154.0	17 Nov 1995	19 Nov 1999	4.0	57.0	4
	185	F	89.7	148.5	17 Nov 1995	29 Mar 1999	3.4	58.8	4
	183	F	94.2	145.0	17 Nov 1995	23 Mar 1999	3.3	50.8	4
									No. of bands past OTC mark
OTC-injected	LN 171	M	118.0	156.0	16 Sep 1996	30 Mar 1999	2.5	38.0	3
	172	M	189.8	187.0	27 Sep 1997	29 Mar 1999	1.5	–2.8	1+
	473	F	104.0	117.0	15 Apr 1999	21 Nov 1999	0.6	13.0	—
	184	M	147.5	152.0	21 Oct 1998	30 Mar 1999	0.4	4.5	—
	204	M	105.0	95.0	23 Mar 1999	23 May 1999	0.2	–10.0	—
	173	F	96.5	96.0	26 Sep 1997	2 Oct 1997	0.02	–0.5	—

shark had one full band and 83% growth of the next band, based on the size of the last full band. This, along with the YOY known-age individuals, confirmed annulus formation and our band interpretation from birth to 11 years of age. Sharks older than age 11 were assumed to have been aged correctly due to a similar interpretation of the bands.

Data analysis

Comparisons of counts between the two readers indicated no appreciable bias (Fig. 4). The coefficient of variation for age 1+ sharks was approximately 15%. In the absence of bias, this level of precision was considered acceptable; thus the counts generated by one reader for the entire set of vertebrae were used for the analyses.

Length-at-age data showed that males and females grow at similar rates until approximately 170 cm FL, at which point the relative growth rate of the males declines (Fig. 5). The change in relative growth between the sexes coincides with the size and age of male maturity (Jensen et al.[4]). Von Bertalanffy growth functions fitted to the vertebral band-pair count data suggested that males attain a smaller maximum size than females (Table 2). The growth rate of females also declined at size at maturity (approximately 218 cm FL; Jensen et al.[4]). The considerable overlap in size at age between the sexes indicated that the difference in growth rate is minor; therefore subsequent comparisons were made for the sexes combined.

Tag-Recapture analysis

A total of 76 porbeagles was recaptured with sufficient information for tag-recapture analysis. Time at liberty ranged from 0.02 to 6.0 years and size at tagging ranged from 78 to 204 cm FL. Sharks were tagged and recaptured in all months of the year. Tagging effort was fairly evenly distributed throughout all months, whereas most recaptures were made between March and May (53%). For both tagging and recapture, January and February were represented by the least data (3% and 1% for tagging and recapture, respectively). More tags were released in December than were recaptured (12% of the tags but only 2% of the recaptures). Most tagged sharks were small (74% <150 cm FL) because the majority were opportunistically tagged onboard commercial fishing vessels. Data from 54 sharks at liberty greater than 0.9 years were used in the Gulland and Holt (1959) analysis, whereas all individuals were used for GROTAG (Francis 1988a).

The results of the likelihood ratio tests with GROTAG (Francis, 1988a) demonstrated that the more complex nonlinear model with five of the six parameters included was the best fit for these data (model 3, Table 3). The high value of s suggests a lack of sufficient information for GROTAG (Francis, 1988a) to distinguish between growth variability and measurement variability (Francis and Mulligan, 1998). The mean annual growth rates at FL= 95 cm and 150 cm were 19.21 cm/yr and 9.52 cm/yr, respectively (Fig. 6). Von Bertalanffy estimates from the Gulland and Holt (1959) and GROTAG (Francis, 1988a) methods produced similar results (Tables 2 and 4).

Length frequency

Analysis of modal length-frequency progressions verified the size at age and growth rate of age-0 and age-1 individuals (Fig. 7). Age-0 fish entered the fishery in July with

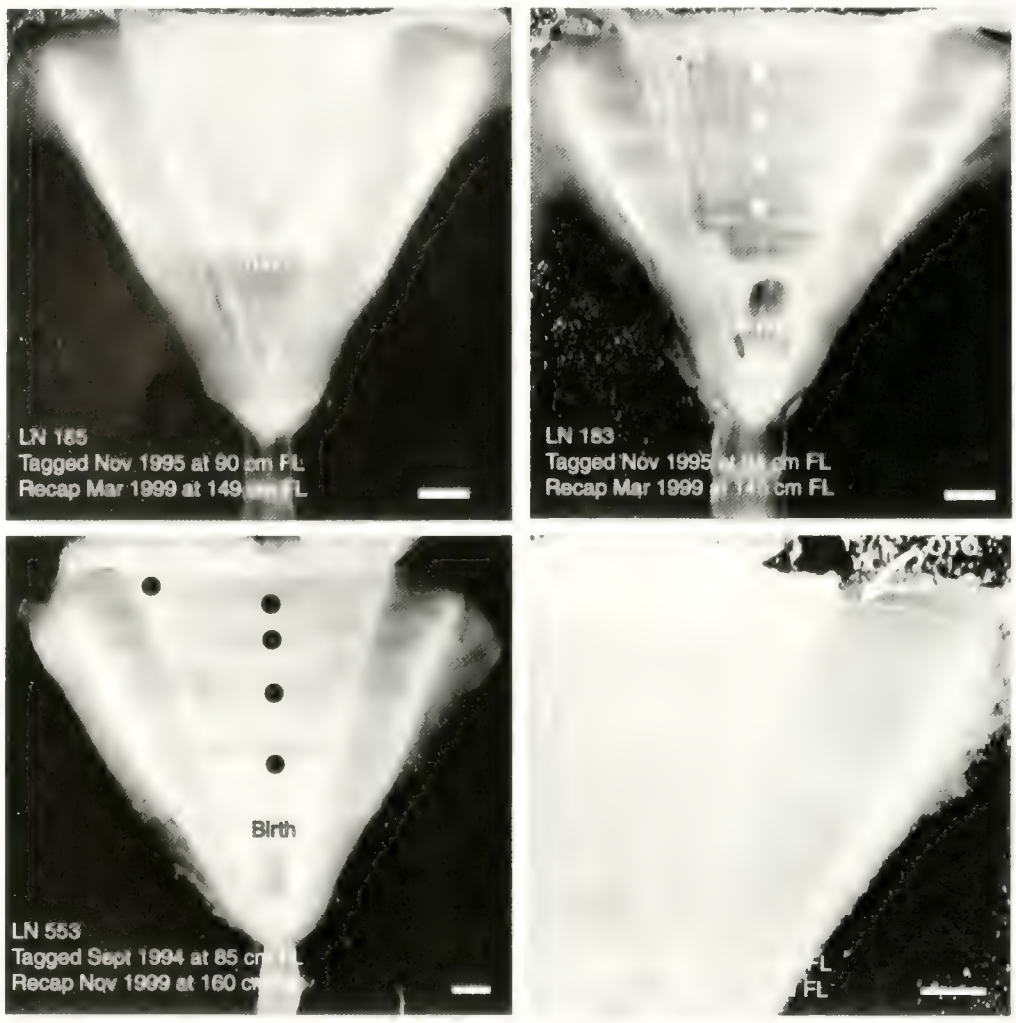

Figure 3

Vertebral sections from recaptures of three known-age porbeagles and one OTC-injected porbeagle. Annuli are indicated, as is the birth mark. Scale bar = 1 mm.

a mean length of 85 cm FL and grew to a mean length of 98 cm FL by December. Age-1 individuals had a mean length of 106 cm FL in April, 113 cm FL in July, and 123 cm FL in December, resulting in an annual growth of 25 cm/yr between December and December. Although larger length modes were occasionally visible, only the age-0 and age-1 modes were clear and unambiguous throughout the year.

The MULTIFAN models that best fitted the 1991 data were the most complex, having variable standard deviations in length and variable seasonal growth. The data with sexes combined had 18 age classes, whereas males and females had 16 and 15 age classes, respectively. The MULTIFAN L_∞ and K von Bertalanffy parameters fell outside the 95% confidence intervals for the tagging and vertebral studies, although the t_0 values did not (Table 2). These differences are reflected in the VBGF curves as compared with the other methods (Fig. 8). The annual growth rate calculated from the MULTIFAN data was consistent with that of the vertebral and tag-recapture analyses at 150 cm FL (Fig. 6). However, the reliability of the MULTIFAN results is questionable given the large number of age classes in the population. The standard error estimates calculated by MULTIFAN were not reported because they were unrealistically low (Francis and Francis, 1992; Francis and Mulligan, 1998).

Longevity

The maximum ages based on vertebral band pair counts were 25 and 24 years for males and females, respectively. These ages likely underestimate longevity, given the long-

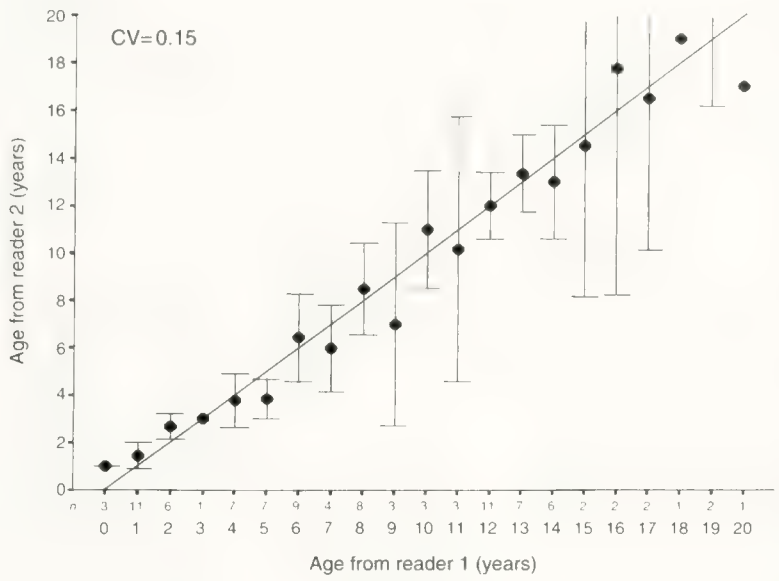

Figure 4

Age bias graph for pair-wise comparison of porbeagle vertebral counts from two independent age readers. Each error bar represents the 95% confidence interval for the mean age assigned by reader 2 to all fish assigned a given age by reader 1. The one to one equivalence line is also presented.

Table 2

Von Bertalanffy growth function parameters and 95% confidence intervals calculated by using vertebral, tag-recapture, and length-frequency methods. Confidence intervals (CI) are not shown for the MULTIFAN parameters. ϕ_1, ϕ_2, are seasonal parameters and t_1 is the time (years) between the theoretical birthday and recruitment to the fishery for the MULTIFAN analyses.

Method		L_∞	K	t_0	n	ϕ_1	ϕ_2	t_1
Vertebral	Combined	289.4	0.066	–6.06	576			
	CI	±16.5	0.010	0.71				
	Male	257.7	0.080	–5.78	283			
	CI	±15.6	0.015	0.92				
	Female	309.8	0.061	–5.90	291			
	CI	±26.2	0.013	0.93				
MULTIFAN	Combined	320.1	0.054	–5.33	13,589	0.95	0.76	0.25
	Male	280.2	0.076	–4.42	7142	0.95	0.92	0.25
	Female	419.0	0.039	–5.45	6269	0.95	0.89	0.25
Gulland and Holt (1959)	Combined	212.5	0.172	–2.21	54			
	CI	±31.7	0.089					
GROTAG	Combined	204	0.194	–2.05	76			

term fishery for this species. Taylor's (1958) method, the age at which 95% of the L_∞ is reached, provided a value of 26 years. However, more realistic estimates of longevity take advantage of estimated mortality rates. Given M=0.10 (Campana et al.[1]), Hoenig's (1983) equation based on multiple species resulted in a longevity estimate of 45 years. The estimate of Campana et al.[2] was species-independent and was calculated by assuming a constant instantaneous rate of mortality = 0.10 in an unfished population. The resulting longevity estimate was 46 years. Each of these methods assumes that M is constant throughout the lifetime of a fish, whereas in fact, it probably increases in sexually mature or senescent fish. Any such increase would result in a lower estimate of longevity. Based on prelim-

Table 3

Log-likelihood function values and parameter estimates for four growth models fitted to porbeagle tagging data by using GROTAG (Francis 1988a). For a significant ($P<0.05$) improvement in fit, the introduction of one extra parameter must increase λ by at least 1.92 (Francis 1988a). * indicates fixed parameters.

Parameter	Symbol (unit)	Model 1	2	3
Log likelihood	λ	−292.04	−291.97	−285.45
Mean growth rates	g_{50} (cm/yr)	19.12	17.92	19.21
	g_{150} (cm/yr)	9.47	8.88	9.52
Measurement error	s (cm)	10.48	10.92	9.43
	m (cm)	0	0.99	1.00
Outliers	p	0*	0*	0.07

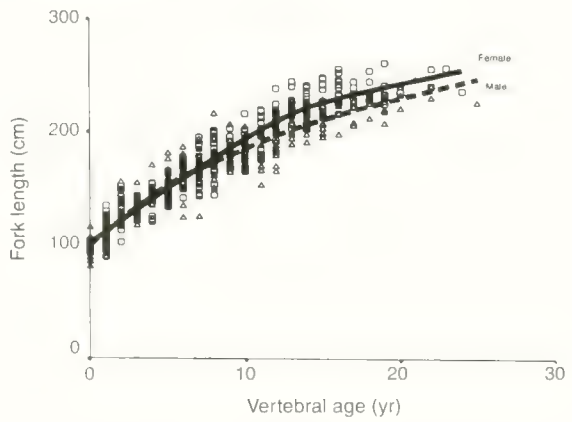

Figure 5

Porbeagle growth data based on vertebral band counts. LOESS curves have been fitted to the data by sex. Open circles represent males, open triangles represent females.

Table 4

Size at age for the porbeagle (*Lamna nasus*) calculated from von Bertalanffy equations based on tag-recapture, length-frequency, and vertebral data.

	Size (cm, FL)			
			Tag-recapture	
Age (years)	Vertebral	MULTIFAN	Gulland and Holt (1959)	GROTAG
0	95	82	67	67
1	107	94	90	91
2	119	106	109	111
3	130	117	126	127
4	140	128	139	141
5	149	138	151	152
6	158	148	161	161
7	166	157	169	169
8	174	165	176	175
9	181	174	181	180
10	188	181	186	184
11	195	189	190	188
12	201	195	194	191
13	206	202	197	193
14	212	208	199	195
15	217	214	201	197
16	221	220	203	198
17	226	225	205	199
18	230	230	206	200
19	233		207	201
20	237		208	201

inary results suggesting an increase in female natural mortality rate (to 0.20) at the age of sexual maturity (Campana[6]), longevity would be estimated at 29 years.

Discussion

Age and growth studies of lamnoids have often been confounded because of the continued debate over the periodicity of band-pair formation. Parker and Stott (1965) first suggested that two growth band pairs formed each year (biannual band-pair deposition) in their study of the basking shark (*Cetorhinus maximus*). Pratt and Casey (1983) assumed biannual band-pair deposition for shortfin mako shark, *Isurus oxyrinchus*, based on consistency with length-frequency and tag-recapture analyses. Branstetter and Musick (1994) also suggested biannual band-pair deposition for the sand tiger shark, *Carcharias taurus*, based on marginal increment analysis (MIA) and examination of aquarium-reared sharks. Cailliet et al. (1983, 1985) assumed annual band-pair deposition for Pacific coast shortfin mako and white sharks, *Carcharodon carcharias*, based on marginal increment analysis. Wintner and Cliff (1999) stated that they could not determine band periodicity using marginal increment analysis in the white shark off the coast of South Africa, although one OTC-injected recapture suggested annual deposition. With the exception of Winter and Cliff (1999), direct validation of band periodicity, such as by OTC injection or by known-age tag-recaptures, has not previously been reported in lamnids. Although several studies have attempted validation with MIA (Branstetter and Musick, 1994; Wintner and Cliff, 1999), this technique is not

[6] Campana, S. 2001. Unpubl. data. Marine Fish Division, Bedford Institute of Oceanography, P.O. Box 1006, Dartmouth, Nova Scotia, Canada B2Y 4A2

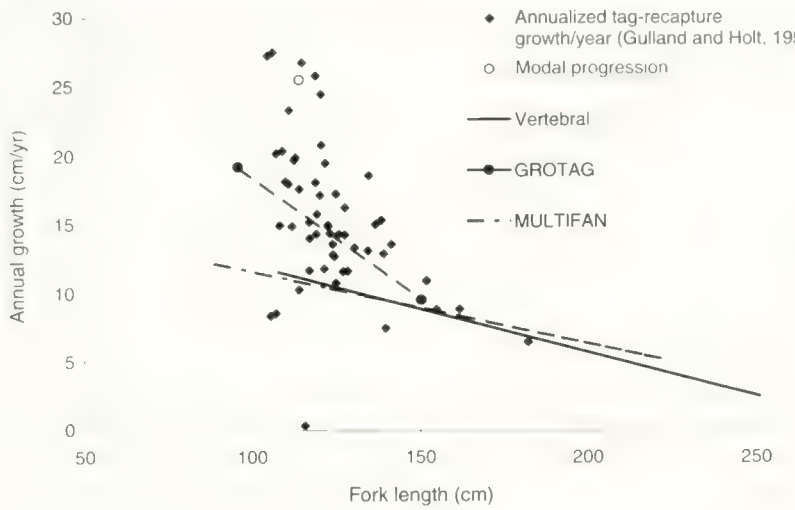

Figure 6

Comparison of the annual growth rate of the porbeagle shark by using multiple aging methods.

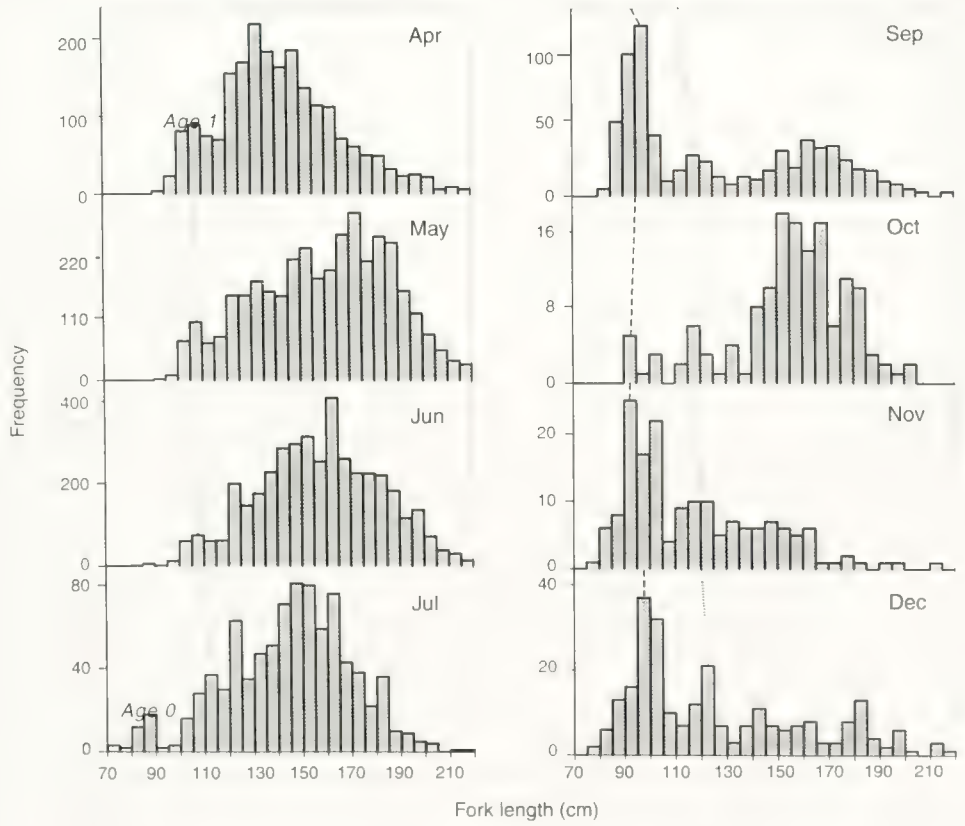

Figure 7

Monthly progressions of age-0 and age-1 length-frequency modes collected by observers in the 1991 Scotian Shelf fishery.

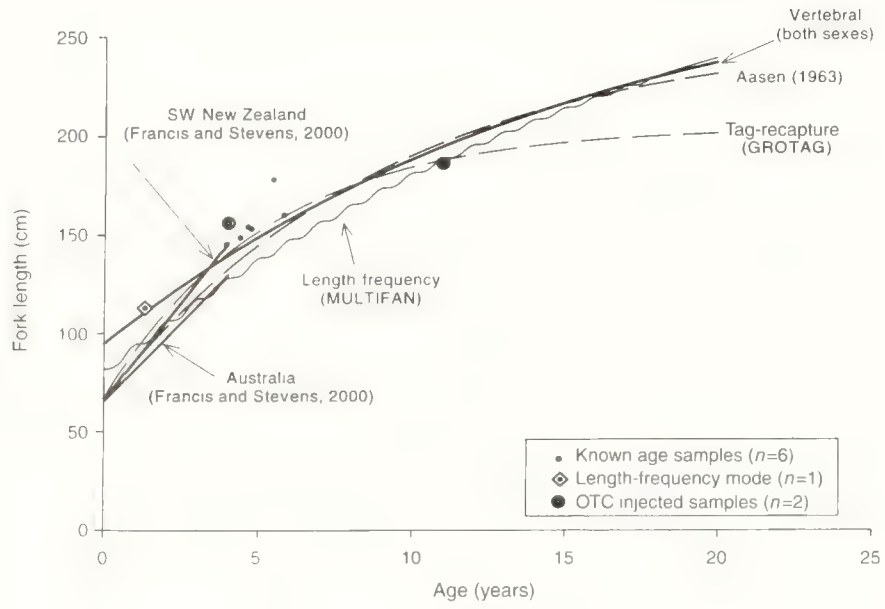

Figure 8

Von Bertalanffy growth curves generated from vertebral data, GROTAG, and MULTIFAN seasonally oscillating parameters, as compared with the length-frequency mode, OTC recaptures, and known-age recaptures (validated). Included for comparison are the von Bertalanffy growth curves of Aasen (1963) and Francis and Stevens (2000).

well suited to slow growing species because the narrowness of the bands at the margin makes it difficult to objectively determine marginal growth.

In the present study, we validated annual band-pair periodicity up to age 11 using recaptures of both OTC-injected and known-age porbeagles. Our data clearly indicated that the vertebral band pairs are deposited annually and that the translucent zone is deposited between November and April.

Validation of an annual frequency of band-pair formation confirms Aasen's (1963) interpretation of the vertebral growth zones in the porbeagle. Our size at birth generated from the vertebral bands (95 cm FL), however, was unrealistically high. This may have been due to our sample of age-0 fish being biased towards the faster growing, larger fish that were recruited first into the fishery. The early portion of our growth curve, corresponding to ages 0 and 1, may therefore have been overestimated (Fig. 8).

Francis (1988b) suggested that growth curves derived from age-length and length-increment data were not directly comparable and that the comparison of growth rates at length was more appropriate. The growth rates at L_{150} were similar for all methods, verifying the growth rate at this size. However, the overall growth curves from the different methods were also similar (Fig. 8). The tag-recapture curve shows a more reasonable early growth than the vertebral curve but levels off well below the observed maximum size. The lower L_∞ and higher K for the tag-recapture method was expected because of the different derivation of the parameters and the absence of recaptured old sharks (Francis, 1988b). The K and t_0 parameters derived from MULTIFAN are close to those obtained by using vertebral ages, and the scatter in the age readings overlaps the MULTIFAN von Bertalanffy curve (Figs. 5 and 8). Although the MULTIFAN L_∞ value was slightly higher than that of the vertebral value (Table 2), a difference at the upper end of these curves was not unexpected because length-frequency models are generally considered unreliable for the older age classes where the modes are not easily defined (Francis and Francis, 1992; Francis, 1997; Francis et al., 1999).

Maturity occurs in the porbeagle at 8 and 13 years of age (174 and 218 cm FL, males and females, respectively; Jensen et al.[4]). Growth for both sexes is similar up to the size of male maturity, whereupon, the male growth rate is reduced. Females continue to grow rapidly until the onset of maturity, at which point their growth slows as well (Fig. 5). Owing to this change in growth rate, males reach a smaller maximum size than females; however, the overall growth rate for both sexes is not substantially different. Additionally, the vertebral L_∞ generated for females is higher than what is being observed in the fishery, suggesting that it has been overestimated and that the combined curve is more appropriate. Aasen[7] (1963) also found no difference in the growth rate between the sexes although the basis for his conclusion is questionable.

Aasen, O. 1961. Some observations on the biology of the porbeagle shark (*Lamna nasus*, L). ICES, C.M. Copenhagen 1961, Near Northern Seas Committee (109):1–7.

Aasen (1963) relied extensively on length-frequency modes to estimate the growth of porbeagle. Although his modes were similar to ours, his interpretation of the age-1 mode differed. Our data indicated that age-0 porbeagle average 85 cm FL in July. Aasen (1963) interpreted this same mode (91 cm FL) as age 1+, thus shifting his ages by one year. Neither Aasen's (1963) modal distribution (his Fig. 4) nor ours, supports the contention that this first mode is age 1+. His classification of these fish as age 1+ was based on size at birth and his opinion that the smallest measured fish were from the age-0 group. There is, however, no mode at this small size. Any age-0 fish born in April and caught between July and September (his sampling period) would certainly be larger than the birth size. Therefore, we feel that these fish represented the faster growing age-0 fish that were large enough to be caught with commercial longline gear. Francis and Stevens (2000) also used length-frequency analysis to estimate the growth rate of porbeagles in the South Pacific. Although their modes were once again comparable to ours, their age 1+ fish were similar in size to our age-0+ fish (Fig. 8). In their view, this first mode represented slow growing age-1 individuals rather than fast growing age-0 individuals. As an alternative explanation, we suggest that the first mode in both the southwest and northeast New Zealand samples represents YOY that have grown during the 4-month sampling period, thus accounting for the apparent absence of individuals close to a birth size. This alternative explanation would also explain why the modal analysis of the Australian sample shows a strong peak at birth and subsequent modes that are similar to ours. If correct, our interpretation of the Francis and Stevens (2000) data would bring their estimates of size at age and growth rate in line with ours. Of course, the comparison of growth rates from such widely separated stocks is difficult, and its value questionable.

Longevity estimates for the porbeagle indicate that they may live for more than 40 years. The maximum time at liberty for any tagged porbeagle is 13 years (Stevens, 1990). The length of this shark when tagged was approximately 120 cm TL (107 cm FL; 1+ years); it was recaptured at an estimated 225 cm FL (age 14+) which would correspond to an age of 16+ years according to our vertebral growth curve. This is substantially less than the oldest observed age from vertebrae (25) and the estimates from the Hoenig (1983) and Campana et al.[2] methods of 45 and 46 years, respectively.

The growth rate and longevity of the porbeagle are similar to those of other lamnids. Wintner and Cliff (1999) calculated a K value of 0.065 for the white shark from the east coast of South Africa, and Cailliet et al. (1985) estimated a K value of 0.058 for the same species off the coast of California. Both estimates are very similar to the K value of 0.066 calculated for porbeagle in our study. Shortfin mako K values have been estimated at 0.072 (Cailliet et al., 1983) and 0.266 (Pratt and Casey, 1983); however the Pratt and Casey value was based on the assumption that two band pairs were deposited annually. Longevity estimates have ranged between 27 years for the California white shark (Cailliet et al., 1985) and 45 years for the shortfin mako in the Pacific (Cailliet et al., 1983).

Comprehensive age and growth studies of pelagic sharks are difficult to implement because many species are highly migratory and are caught sporadically as part of seasonal fisheries. Thus, aging studies of pelagic sharks have usually been less rigorous than desired, despite the oft-repeated call for age validation (Beamish and McFarlane, 1983; Cailliet et al., 1986, Cailliet, 1990). Previous studies on pelagic species such as the blue shark (Stevens, 1975; Cailliet et al., 1983), white shark (Cailliet et al., 1985), thresher (Cailliet et al., 1983), shortfin mako (Cailliet et al, 1983), pelagic thresher (Liu et al., 1999), oceanic whitetip shark (Lessa et al., 1999), and porbeagle (Aasen, 1963; Francis and Stevens, 2000), have included analyses of ages determined by vertebral or length-frequency analyses (or by both methods), but none of the age interpretations were validated. Wintner and Cliff (1999) used vertebral counts and had one OTC-injected recapture but were unable to provide validation or consistency with other methods. Pratt and Casey (1983) aged the shortfin mako by using four methods (temporal analysis of length-month information, tag-recapture data, length-frequency data, and vertebral band counts) but could not validate their age interpretations. The conclusion that band pairs were deposited biannually was based on vertebrae from four tag-recaptures and consistency between methods. Skomal (1986) aged the blue shark in the western North Atlantic using a combination of vertebral, length frequency and tag-recapture methods for verification. Although Skomal (1986) had two OTC-injected recaptures, they provided conflicting results for validation. The present study is the first that has used validated vertebral band-pair counts in conjunction with length-frequency and tag-recapture analyses to provide consistent and accurate age estimates for a pelagic shark species. We suggest that a similar approach would be useful in studies of other pelagic shark species.

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Food habits and consumption rates of common dolphinfish (*Coryphaena hippurus*) in the eastern Pacific Ocean

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Abstract—An ecosystem approach to fisheries management requires an understanding of the impact of predatory fishes on the underlying prey resources. Defining trophic connections and measuring rates of food consumption by apex predators lays the groundwork for gaining insight into the role of predators and commercial fisheries in influencing food web structure and ecosystem dynamics. We analyzed the stomach contents of 545 common dolphinfish (*Coryphaena hippurus*) sampled from 74 sets of tuna purse-seine vessels fishing in the eastern Pacific Ocean (EPO) over a 22-month period. Stomach fullness of these dolphinfish and digestion state of the prey indicated that diel feeding periodicity varied by area and may be related to the digestibility and energy content of the prey. Common dolphinfish in the EPO appear to feed at night, as well as during the daytime. We analyzed prey importance by weight, numbers, and frequency of occurrence for five regions of the EPO. Prey importance varied by area. Flyingfishes, epipelagic cephalopods, tetraodontiform fishes, several mesopelagic fishes, *Auxis* spp., and gempylid fishes predominated in the diet. Ratios of prey length to predator length ranged from 0.014 to 0.720. Consumption-rate estimates averaged 5.6% of body weight per day. Stratified by sex, area, and length class, daily rations ranged up to 9.6% for large males and up to 19.8% for small dolphinfish in the east area (0–15°N, 111°W–coastline). Because common dolphinfish exert substantial predation pressure on several important prey groups, we concluded that their feeding ecology provides important clues to the pelagic food web and ecosystem structure in the EPO.

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Dolphinfishes (*Coryphaena hippurus* and *C. equiselis*) are abundant, wide-ranging, epipelagic predators in tropical and subtropical oceans (Palko et al., 1982). They support important commercial, artisanal, and recreational fisheries in several regions (Beardsley, 1967; Oxenford and Hunte, 1986; Patterson and Martinez, 1991; Campos et al., 1993; Norton and Crooke, 1994; Lasso and Zapata, 1999). Dolphinfishes are also a large component of the bycatches of the tuna purse-seine and longline fisheries in the Pacific Ocean (Lawson, 1997; IATTC, 1999). They are commonly found near natural and artificial floating objects (Kojima, 1956; Hunter and Mitchell, 1966; Gooding and Magnuson, 1967; Wickham et al., 1973), a trait which facilitates their capture.

Calls have been issued for developing an ecological approach to fisheries management, taking greater note of species interactions and underlying ecosystem dynamics (FAO, 1995; Larkin, 1996; Mangel et al., 1996; Botsford et al., 1997). Removal of predator biomass by commercial fishing represents a "top-down" disturbance of the system. Selective exploitation of apex predators can have profound effects on pelagic ecosystems because of the removal of predation pressure (Essington et al., in press) and because of top-down, trophic-cascade effects (Shiomoto et al., 1997; Estes et al., 1998; Verheye and Richardson, 1998). An understanding of how top-down processes influence the dynamics of marine communities derives from a basic understanding of the trophic connections and rates of food consumption of the predators. Although four studies have provided limited data on the food habits of dolphinfishes in coastal areas of the eastern Pacific Ocean (EPO) (Hida, 1973; Campos et al., 1993; Aguilar-Palomino et al., 1998; Lasso and Zapata, 1999), little is known of the predation dynamics of dolphinfishes over the majority of their oceanic habitat.

Common dolphinfish (*C. hippurus*) are renowned for their rapid rates of growth and metabolism. In Hawaiian waters, common dolphinfish have attained average lengths of 120 cm and weights of 12.5 kg at 12 months of age (Uchiyama et al., 1986). Standard metabolic rates of common dolphinfish are comparable to those of yellowfin (*Thunnus albacares*) and skipjack (*Katsuwonus pelamis*) tunas (Benetti et al., 1995). All three species have large surface areas and thin blood-water interfaces in their gills, morphological features that permit high oxygen diffusion capacity and elevated metabolic rates (Brill, 1996). High energy requirements imply that predators like dolphinfish can account for important amounts of tertiary production removed from an ecosystem (Essington et al., in press), but rates of food consumption by dolphinfish in nature have not been measured.

The objectives of our study were to define the trophic relations of the com-

mon dolphinfish, and their prey in both coastal and oceanic areas of the EPO and to provide preliminary estimates of their daily rates of food consumption.

Materials and methods

The dolphinfish were caught by tuna purse-seine vessels of Colombian, Mexican, Panamanian, and Venezuelan registry from December 1992 through September 1994. The fish were caught as bycatch of the purse-seine fishery for tunas associated with dolphins, with floating objects, and as unassociated schools ("schoolfish"). In dolphin sets, the net is deployed around aggregations of primarily yellowfin tuna and spotted or spinner dolphins (*Stenella attenuata* or *S. longirostris*) (or both dolphin species) after a high-speed chase by speedboats. Floating-object sets are made by encircling flotsam, commonly tree parts and artificial fish-aggregating devices (FADs), and associated fauna with the purse seine, usually in the early morning. Schoolfish are detected by seabird activity and disturbance of the water surface caused by the fish swimming just below. The species composition and size and age distribution of the fauna are distinctly different for the three aggregation types and fishing strategies (Hall, 1998).

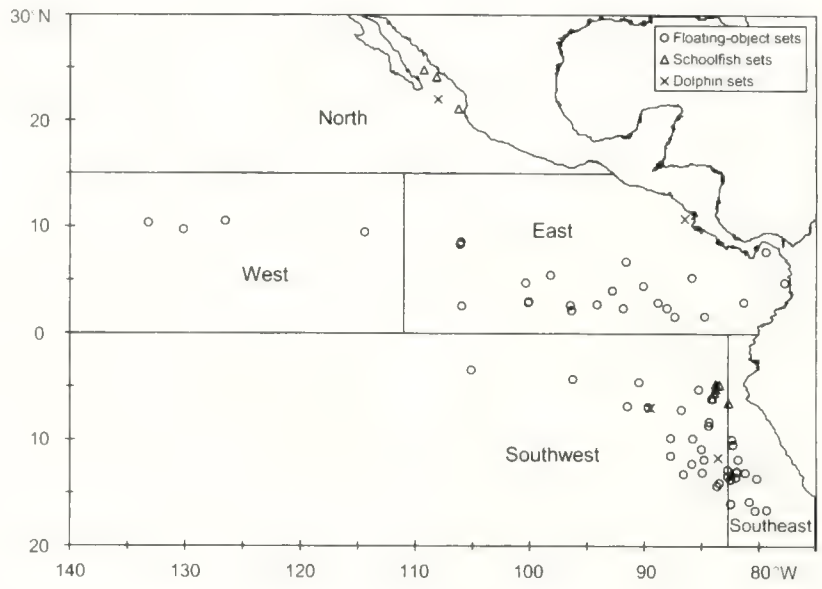

Figure 1

Locations where common dolphinfish samples were caught by three types of purse-seine sets. We stratified the data into the five areas shown.

Stomach samples

Common dolphinfish stomach samples were taken at sea by observers of the Inter-American Tropical Tuna Commission (IATTC). The purse-seine sets yielding the dolphinfish samples were distributed across the geographical range of the EPO tuna fishery at that time (Fig. 1). We obtained samples from 74 purse-seine sets over a 22-month period: 61 sets (82%) were made on floating objects; 4 sets were made on dolphins; and 9 sets were made on unassociated tuna. On board the vessels, the observers measured the fork length (mm) of each dolphinfish, determined the sex if possible, and excised and immediately froze the stomachs. In the laboratory, we thawed the stomachs and visually estimated the stomach fullness as a percentage of the stomach capacity. Then, we identified the stomach contents to the lowest taxon possible, weighed them to the nearest gram, and enumerated them when individuals were recognizable. The counts of paired structures, such as cephalopod mandibles and fish otoliths, were divided by two to estimate numbers of prey. We categorized the digestion state of the prey: 1 = intact or nearly intact; 2 = soft parts partially digested; 3 = whole or nearly whole skeletons without flesh (or comparable state for nonfish taxa); and 4 = only hard parts remaining (primarily fish otoliths and cephalopod mandibles). We measured the length, or maximum dimension of individual prey to the nearest mm, if sufficiently intact. For cephalopods, we recorded the mantle length excluding tentacles.

Identifying the prey depended on the digestion state of the remains. We used the following keys to identify fish prey in digestion state 1: Jordan and Evermann (1896), Meek and Hildebrand (1923), Parin (1961), Miller and Lea (1972), Thomson et al. (1979), Allen and Robertson (1994), and Fischer et al. (1995b and 1995c). When the fishes were digested to state 2 or 3 we used taxonomic keys of vertebral characteristics (e.g. Clothier, 1950; Monod, 1968; Miller and Jorgenson, 1973) and compared skeletons of whole fishes collected in the EPO. We identified the crustacean prey from exoskeleton remains using the keys of Garth and Stephenson (1966), Brusca (1980), and Fischer et al. (1995a). We identified cephalopod prey from mandible remains (Clarke, 1962; Iverson and Pinkas, 1971; Wolff, 1982; Clarke, 1986). The fish collections at Scripps Institution of Oceanography and the Natural History Museum of Los Angeles County, and the cephalopod collection at the Santa Barbara Museum of Natural History were used to compare and validate prey identifications.

Data analysis

We analyzed the diet data by calculating three diet indices for each prey taxon. We calculated gravimetric importance of the prey ($\%W$) as percentages of the total prey weights, numerical importance ($\%N$) as percentages of total counts, and frequency of occurrence as the number of dolphinfish stomachs that contained a particular prey. We calculated percent occurrence ($\%O$) as a percentage of all the dolphinfish sampled, regardless of whether their stomachs contained food. We present these three indices by prey taxon in detailed tables, summarized at several

levels of taxonomic resolution. To facilitate analysis, we also grouped the prey taxa by order (e.g. Tetraodontiformes), family (e.g. Carangidae), genus (e.g. *Auxis* spp.), or functional group (e.g. flyingfishes).

Because the three diet indices provide different insights into predation habits, we applied a graphical representation of these measures, proposed by Cortés (1997), to help interpret the data. We made three-dimensional scatter plots of $\%O$, $\%W$, and $\%N$ for all samples and for the data pooled by sampling area to help evaluate the degree of dominance of particular prey and the feeding strategy (generalized vs. specialized) of the dolphinfish. Although we measured the three components of the index of relative importance (IRI) (Pinkas et al., 1971), we did not calculate IRI values because the index is dependent upon the taxonomic resolution of the prey (Hansson, 1998). Also, for a predator that consumes a large size range of prey (see heading "Prey size," below), the IRI is overly influenced by numerous small prey.

We examined diel feeding characteristics by stratifying the data according to stomach fullness of the predator and digestion state of the prey. The scheme for grouping the data, patterned after Calliet (1976), is diagrammed in Figure 2. Prey in digestion states 1 and 2 were categorized as from "recent" feeding events, whereas prey in states 3 and 4 were categorized as from "previous" feedings. These two strata were further subdivided according to stomach fullness. Prey from stomachs ≤50% full were categorized as "low" fullness or empty, whereas those from stomachs >50% full were categorized as "high" fullness (Fig. 2). We plotted the percent occurrence of the prey items in these four digestion and fullness strata by area and the time of day the sets were made: "early morning" (05:12–09:00), "late morning" (09:01–12:00), "early afternoon" (12:01–15:00), and "late afternoon" (15:01–18:16 hours).

We fitted regression trees (Breiman et al., 1984) to the gravimetric data for each prey group to detect statistically important differences by area and dolphinfish size. Regression trees are well suited for detecting and extracting important relations and complex interactions in multivariate ecological (De'ath and Fabricius, 2000) and fisheries data (Watters and Deriso, 2000). We used a two-step process. For both steps, the $\%W$ of each prey group in the stomach contents was the response variable. For the first step, defining area strata (see next paragraph), we used latitude and longitude as the predictor variables. For the second step, modeling the importance of area and dolphinfish size in explaining variation in the $\%W$ for each prey group, we used area designations (north, west, east, southwest, and southeast) and fork length as the predictor variables. We used the tree functions in S-Plus (MathSoft Inc., 1999) and cross-validation to prune fully grown trees so that only important splits remained. Prediction errors were used as pruning criteria (Breiman et al., 1984; De'ath and Fabricius, 2000).

We stratified the data by area (Fig. 1) according to two criteria. Latitude divisions at 15°N and 0° were based on the spatial and seasonal heterogeneity of the purse-seine sets that provided the samples. All the sets sampled from May through November each year were made north of the equator, and most sets sampled during December through April were made south of the equator. Also, the regression trees indicated that latitude and longitude were important in explaining the variability in the gravimetric data for several prey taxa. Epipelagic-cephalopod taxa were most important in the diet of the common dolphinfish caught east of 82°41′W and south of 1° 46′S, and flyingfishes were most important in the diet of those caught west of 81°W. Therefore, we stratified the data from south of the equator into "southwest" and "southeast" areas separated at 82°41′W (Fig. 1). Similarly, we stratified the data from samples collected between 0° and 15°N into "west" and "east" areas divided at 111°W because a regression tree fitted to the gravimetric data for the Tetraodontiformes indicated that this meridian was important in explaining variation in $\%W$ for this taxon. Tetraodontiformes were more important in the diet of the fish caught west of 111°W.

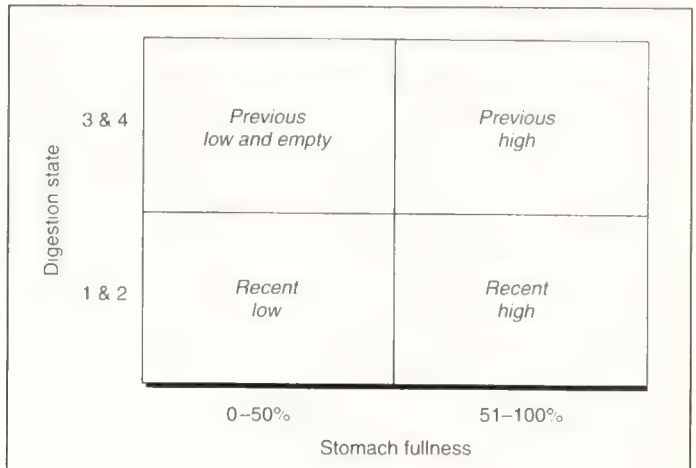

Figure 2

Schematic diagram showing prey digestion-state and predator stomach-fullness criteria for four categories used to analyze diel feeding characteristics of common dolphinfish in the eastern Pacific Ocean.

Consumption rates

We employed a method described by Olson and Mullen (1986) to calculate preliminary estimates of daily rates of food consumption by common dolphinfish. The model predicts feeding rate ($\hat{r}$, grams per hour) by dividing the mean weight of the stomach contents per predator ($\overline{W}$, grams) by the integral (A, proportion × hours=hours) of the function that best fits experimental gastric evacuation data. For a predator that consumes a variety of prey that are evacuated at different rates,

$$\hat{r} = \sum_{i=1}^{I} \frac{\overline{W}_i}{A_i}, \qquad (1)$$

where subscripts i refer to each of I prey types.

Table 1

Numbers of common dolphinfish sampled by size, sex, and area with undigested food in their stomachs (first number) and with empty stomachs or trace amounts of hard parts (in parentheses).

	Sex			Area					
Fork length (mm)	Males	Females	Undetermined sex	North	West	East	Southwest	Southeast	Total no. of dolphinfish
417–650	2 (14)	14 (39)	4 (5)	0 (1)	0 (3)	4 (24)	16 (21)	0 (9)	20 (58)
651–800	12 (21)	48 (47)	8 (3)	1 (0)	2 (9)	14 (11)	37 (47)	14 (4)	68 (71)
801–950	24 (29)	51 (70)	11 (7)		11 (11)	13 (13)	43 (60)	19 (22)	86 (106)
951–1100	26 (25)	15 (21)	3 (1)		0 (2)	10 (10)	19 (19)	15 (16)	44 (47)
1101–1250	9 (6)	10 (6)	2 (1)	2 (0)		10 (5)	5 (1)	4 (7)	21 (13)
1251–1770	6 (1)	1 (1)	0 (1)			1 (1)	2 (1)	4 (1)	7 (3)
Total	79 (96)	139 (184)	29 (18[1])	3 (1)	13 (25)	52 (64)	122 (150[1])	56 (59)	246 (299[1])

[1] Including one dolphinfish with no length or sex data.

Daily meal is $\hat{r}$ multiplied by 24 h for fish that feed both day and night. Daily ration is daily meal expressed as a percent of body weight. We estimated the body weight of each dolphinfish from the length, according to the relationships of Lasso and Zapata (1999):

$$M = aL^b, \quad (2)$$

where M = body weight (g); and
L = fork length (cm).

They estimated that $a = 0.0406, 0.0420$, and 0.0224, and $b = 2.6588, 2.6328$, and 2.78 for males, females, and common dolphinfish of undetermined sex, respectively. We estimated daily consumption rates for dolphinfish of six size strata by sex and area.

The time-course of gastric evacuation has not been adequately described for dolphinfishes. This fact prevents a rigorous analysis of consumption rates using stomach-contents data. However, we provide preliminary, first-order estimates of daily rations of common dolphinfish because this information is important for analyses of ecosystem effects of fishing (see "Discussion" section). A preliminary experiment indicated that the gastric evacuation rate for squid tissue by juvenile dolphinfish is comparable to that for squid by yellowfin tuna. Five juvenile common dolphinfish passed pellets of moist squid tissue through the digestive tract in 6–8 h at 27°C (Suzuki, 1992). The fastest gastric evacuation times for squid (*Loligo opalescens*) voluntarily ingested by yellowfin tuna (mean L=36.2 cm) in the laboratory were about 8 h at 23.5–25.5°C (Olson and Boggs, 1986). We assume, therefore, that gastric evacuation rates measured for yellowfin tuna are adequate for estimating daily rations of dolphinfish. We assigned values of A (Eq. 1) for squid (4.48), mackerel (*Scomber japonicus*) (5.29), smelt (*Hypomesus pretiosus*) (4.12), and nehu (*Stolephorus purpureus*) (2.24), and the mean for four experimental food species (3.77) determined by Olson and Boggs (1986) to the various prey taxa of common dolphinfish, as they did for yellowfin tuna. We omitted the data for the trace hard parts (cephalopod mandibles and fish otoliths), which apparently accumulate in the stomachs, when calculating consumption rates because of the possibility that these remained from predation on previous days.

Results

Stomach samples were obtained from 545 dolphinfish: 175 males, 323 females, and 47 of undetermined sex. Two hundred and forty-six specimens had fresh or partially digested food remains in their stomachs, 274 had empty stomachs, and 25 had only trace amounts of digestion-resistant hard parts (cephalopod mandibles and fish otoliths). We present the sample sizes by sex and area in Table 1 and the detailed prey-composition data by area in Tables 2–4. We analyzed the prey composition data by sex but did not discover important differences or trends.

Few samples were obtained in the north and west areas. Therefore, we briefly summarize those data here and in Tables 2–4 and do not include them in the detailed treatments of diel feeding periodicity, diet measures by area, and size-specific predation. Only four common dolphinfish were sampled in the north area, three from sets on schoolfish and one from a set on dolphins. Three of the stomach samples contained food and one was empty. A large dolphinfish (1149 mm) had recently eaten a large squid (*Sthenoteuthis oualaniensis*) in the early morning. Another large fish (1239 mm) had a full stomach containing 7 fresh *Coryphaena equiselis* in the late afternoon. Both fish had been collected from schoolfish sets. A smaller dolphinfish (768 mm) from a dolphin set in the late afternoon had remains of various taxa, principally *C. equiselis*, flyingfishes, and galatheid red crabs (*Pleuroncodes planipes*) in advanced states of digestion. In addition, a 564-mm dolphinfish from a schoolfish set was found to have an empty stomach.

Thirty-eight common dolphinfish were sampled in the west area from 4 sets on floating objects between 05:40 and

Table 2

Taxonomic composition in %*W* of the prey of common dolphinfish from five areas of the eastern Pacific Ocean (Fig. 1) and from all areas combined. Weights do not include hard parts (cephalopod mandibles and fish otoliths). Prey category codes are as follows: EC = epipelagic cephalopods, MC = mesopelagic cephalopods, Cr = Crustacea, MiF = miscellaneous fishes, MsF = mesopelagic fishes, F = flyingfishes, Co = Coryphaenidae, Ca = Carangidae, G = Gempylidae, A = *Auxis* spp., YT = yellowfin tuna, N = Nomeidae, T = Tetraodontiformes. A_i is the integral of the function fitted to experimental gastric evacuation data and is used to calculate consumption rates (Eq. 1). Area codes are N = north, W = west, E = east, SW = southwest, SE = southeast.

Taxon	Category	Assumed A_i	Area					
			N	W	E	SW	SE	All
Phylum Mollusca		4.48	16.35	2.54	9.48	21.69	82.73	32.20
Class Cephalopoda		4.48	16.35	2.54	9.48	21.69	82.73	32.19
Order Teuthoidea		4.48	16.35	2.54	9.48	21.66	81.84	31.91
Family Enoploteuthidae	EC	4.48		*		*	*	*
Abraliopsis falco	EC	4.48		*		*	*	*
Family Mastigoteuthidae	MC	4.48			0.15	0.01		0.04
Mastigoteuthis spp.	MC	4.48			0.15	0.01		0.04
Family Ommastrephidae	EC	4.48	16.35	2.54	5.47	21.40	81.84	30.72
Dosidicus gigas	EC	4.48		2.54	0.78	5.08	70.73	19.27
Sthenoteuthis oualaniensis	EC	4.48	16.35		4.69	16.32	11.11	11.45
Family Onychoteuthidae	EC	4.48			3.26	0.09		0.91
Onychoteuthis banksii	EC	4.48			3.26	0.09		0.91
Onychoteuthis spp.	EC	4.48				*		*
Family Pholidoteuthidae	EC	4.48				*		*
Pholidoteuthis boschmani	EC	4.48						
Family Thysanoteuthidae	EC	4.48			*	0.17		0.07
Thysanoteuthis rhombus	EC	4.48				0.17		0.07
Order Octopoda	EC	4.48		*	*	0.02	1.16	0.29
Family Tremoctopodidae	EC	4.48					1.16	0.28
Tremoctopus violaceus	EC	4.48					1.16	0.28
Family Argonautidae	EC	4.48		*	*	0.02	*	0.01
Argonauta spp.	EC	4.48		*	*	0.02	*	0.01
Family Bolitaenidae	MC	4.48		*		*		*
Japetella diaphana	MC	4.48		*		*		*
Phylum Arthropoda		3.37	1.39		3.26	0.01		0.94
Class Crustacea	Cr	3.37	1.39		3.26	0.01		0.94
Order Decapoda	Cr	3.37	1.39		3.26	0.01		0.94
Family Galatheidae	Cr	3.37	1.39					0.06
Pleuroncodes planipes	Cr	3.37	1.39					0.06
Family Penaeidae	Cr	3.37			0.61			0.16
Family Portunidae	Cr	3.37			2.65			0.71
Portunus xantusii	Cr	3.37			2.65			0.71
Phylum Chordata		4.12	82.26	97.46	87.24	78.30	17.00	66.84
Class Osteichthyes		4.12	82.26	97.46	87.24	78.30	17.00	66.84
Order Clupeiformes	MiF	4.12			0.08			0.02
Family Engraulidae	MiF	4.12			0.08			0.02
Order Stomiiformes	MsF	2.24			0.48	4.53		2.01
Family Phosichthyidae	MsF	2.24			0.48	4.53		2.01
Vinciguerria lucetia	MsF	2.24			0.48	4.53		2.01
Order Myctophiformes	MsF	2.24	0.07	4.26	3.11			0.97
Family Myctophidae	MsF	2.24	0.07	4.26	3.11	*		0.97
Benthosema panamense	MsF	2.24		*				*

continued

Table 2 (continued)

Taxon	Category	Assumed A_i	Area					
			N	W	E	SW	SE	All
Myctophum aurolaternatum	MsF	2.24			0.97			0.26
Myctophum nitidulum	MsF	2.24			*			*
Symbolophorus spp.	MsF	2.24		4.26	2.14	*		0.71
Order Lampridiformes	MsF	5.29				3.04		1.27
Family Trachipteridae	MsF	5.29				3.04		1.27
Desmodesma polystictum	MsF	5.29				3.04		1.27
Order Beloniformes			1.59	26.50	49.58	31.64	9.29	29.58
Family Belonidae	MiF	5.29			0.26		1.34	0.39
Strongylura spp.	MiF	5.29			0.26		1.34	0.39
Family Exocoetidae	F	4.12		16.14	30.77	28.43	7.95	22.48
Cheilopogon furcatus	F	4.12				0.66		0.27
Cheilopogon spilonotopterus	F	4.12				0.12		0.05
Cheilopogon spp.	F	4.12		10.96	0.53	3.59	2.94	2.68
Exocoetus monocirrhus	F	4.12			19.19	0.69	1.09	5.69
Exocoetus volitans	F	4.12		5.18	5.34	17.64	1.58	9.31
Exocoetus spp.	F	4.12			0.92	5.04	1.81	2.77
Hirundichthys speculiger	F	4.12			3.17		0.53	0.98
Prognichthys spp.	F	4.12			1.22	0.47		0.52
Family Hemiramphidae	F	4.12	1.59	10.36	18.55	3.21		6.71
Oxyporhamphus micropterus	F	4.12	1.59	10.36	18.55	3.21		6.71
Order Perciformes			80.11		32.60	36.32	5.76	28.90
Family Echeneidae	MiF	3.77				2.48		1.03
Rhombochirus osteochir	MiF	3.77				2.48		1.03
Family Coryphaenidae	Co	5.29	80.11		1.43	2.36	0.20	5.08
Coryphaena equiselis	Co	5.29	80.11			0.01		3.67
Coryphaena hippurus	Co	5.29				1.23		0.51
Family Carangidae	Ca	5.29			0.34	5.48		2.37
Naucrates ductor	Ca	5.29			0.34	3.88		1.71
Family Gempylidae	G	5.29			16.53	3.93	0.01	6.07
Gempylus serpens	G	5.29			16.53	3.93	0.01	6.07
Family Scombridae	MiF	5.29			13.18	15.97	5.54	11.50
Acanthocybium solandri	MiF	5.29			0.04			0.01
Auxis spp.	A	5.29			10.15	15.78		9.29
Euthynnus lineatus	MiF	5.29			1.50			0.40
Thunnus spp.	YT	5.29			1.49	0.19	5.54	1.80
Family Nomeidae	N	2.24			1.12	6.11		2.84
Cubiceps pauciradiatus	N	2.24			1.12	6.11		2.84
Order Tetraodontiformes	T	3.77	0.49	66.70	1.38	2.77		3.63
Family Balistidae	T	3.77	0.21	38.78				1.22
Xantichthys mento	T	3.77		38.78				1.21
Family Ostraciidae	T	3.77		25.99				0.81
Lactoria diaphanum	T	3.77		25.99				0.81
Family Tetraodontidae	T	3.77	0.28	1.93	1.38	2.77		1.60
Lagocephalus lagocephalus	T	3.77	0.28	1.93	1.38	2.77		1.60
Unidentified fishes	MiF	3.77					1.95	0.47
Total prey weight (g)			1443	985	8459	13,118	7523	31,527

* Only trace quantities of hard parts were present

Table 3

Taxonomic composition in %*N* of the prey of common dolphinfish from five areas of the eastern Pacific Ocean (Fig. 1) and from all areas combined. Numbers include hard parts (cephalopod mandibles and fish otoliths) divided by two. Numbers are not complete for some taxa because sometimes prey could not be enumerated due to being in an advanced digestion state. Area codes are N = north, W = west, E = east, SW = southwest, SE = southeast.

	Area					
Taxon	N	W	E	SW	SE	All
Phylum Mollusca	2.17	12.36	24.46	19.97	87.35	37.43
Class Cephalopoda	2.17	12.36	24.46	19.97	87.35	37.37
Order Teuthoidea	2.17	7.87	24.21	16.93	85.25	35.27
Family Enoploteuthidae		1.12		3.62	0.23	1.62
Abraliopsis falco		1.12		3.62	0.23	1.62
Family Mastigoteuthidae			0.24	0.29		0.18
Mastigoteuthis spp.			0.24	0.29		0.18
Family Ommastrephidae	2.17	6.74	4.60	11.87	85.01	28.20
Dosidicus gigas		6.74	2.91	9.99	82.20	26.23
Sthenoteuthis oualaniensis	2.17		1.69	1.74	2.81	1.92
Family Onychoteuthidae			18.16	0.72		4.79
Onychoteuthis banksii			18.16	0.58		4.73
Onychoteuthis spp.				0.14		0.06
Family Pholidoteuthidae				0.29		0.12
Pholidoteuthis boschmani				0.29		0.12
Family Thysanoteuthidae			0.24	0.14		0.12
Thysanoteuthis rhombus			0.24	0.14		0.12
Order Octopoda		4.49	0.24	3.04	2.11	2.10
Family Tremoctopodidae					0.94	0.24
Tremoctopus violaceus					0.94	0.24
Family Argonautidae		2.25	0.24	2.75	1.17	1.62
Argonauta spp.		2.25	0.24	2.75	1.17	1.62
Family Bolitaenidae		2.25		0.29		0.24
Japetella diaphana		2.25		0.29		0.24
Phylum Arthropoda	69.57		12.38	0.14		5.05
Class Crustacea	69.57		12.38	0.14		5.05
Order Decapoda	69.57		12.38	0.14		5.03
Family Galatheidae	69.57					1.92
Pleuroncodes planipes	69.57					1.92
Family Penaeidae			1.69			0.42
Family Portunidae			10.65			2.63
Portunus xantusii			10.65			2.63
Phylum Chordata	2.17	87.64	62.95	79.88	12.65	57.31
Class Osteichthyes	2.17	87.64	62.95	79.88	12.65	57.31
Order Clupeiformes			0.48			0.12
Family Engraulidae			0.48			0.12
Order Stomiiformes			*	41.97		17.37
Family Phosichthyidae			*	41.97		17.37
Vinciguerria lucetia			*	41.97		17.37
Order Myctophiformes	2.17	57.30	14.77	0.14		6.83
Family Myctophidae	2.17	57.30	14.77	0.14		6.83
Benthosema panamense		16.85				0.90

continued

Table 3 (continued)

Taxon	Area					
	N	W	E	SW	SE	All
Myctophum aurolaternatum			3.39			0.84
Myctophum nitidulum			3.15			0.78
Symbolophorus spp.		40.45	8.23	0.14		4.25
Order Lampridiformes				0.58		0.24
Family Trachipteridae				0.58		0.24
Desmodesma polystictum				0.58		0.24
Order Beloniformes	4.35	11.24	36.08	29.52	10.77	24.61
Family Belonidae			0.24		0.23	0.12
Strongylura spp			0.24		0.23	0.12
Family Exocoetidae		6.74	19.13	26.34	10.54	18.68
Cheilopogon furcatus				0.29		0.12
Cheilopogon spilonotopterus				0.29		0.12
Cheilopogon spp.		2.25	0.48	1.74	2.34	1.56
Exocoetus monocirrhus			8.96	0.87	0.47	2.69
Exocoetus volitans		4.49	5.33	13.31	3.51	7.96
Exocoetus spp.			1.94	9.55	3.98	5.45
Hirundichthys speculiger			1.45		0.23	0.42
Prognichthys spp.			0.97	0.29		0.36
Family Hemiramphidae	4.35	4.49	16.71	3.18		5.81
Oxyporhamphus micropterus	4.35	4.49	16.71	3.18		5.81
Order Perciformes	17.39		10.41	6.80	1.64	6.29
Family Echeneidae				0.29		0.12
Rhombochirus osteochir				0.29		0.12
Family Coryphaenidae	17.39		0.24	0.72	0.47	0.96
Coryphaena equiselis	17.39			0.14		0.54
Coryphaena hippurus				0.29		0.12
Family Carangidae			0.97	1.88		1.02
Naucrates ductor			0.97	1.45		0.84
Family Gempylidae			3.63	1.01	0.47	1.44
Gempylus serpens			3.63	1.01	0.47	1.44
Family Scombridae			1.69	1.88	0.70	1.38
Acanthocybium solandri			0.24			0.06
Auxis spp.			0.97	1.74		0.96
Euthynnus lineatus			0.24			0.06
Thunnus spp			0.24	0.14	0.70	0.30
Family Nomeidae			3.87	1.01		1.38
Cubiceps pauciradiatus			3.87	1.01		1.38
Order Tetraodontiformes	4.35	19.10	1.21	0.72		1.74
Family Balistidae	2.17	2.25				0.18
Xantichthys mento		2.25				0.12
Family Ostraciidae		15.73				0.84
Lactoria diaphanum		15.73				0.84
Family Tetraodontidae	2.17	1.12	1.21	0.72		0.72
Lagocephalus lagocephalus	2.17	1.12	1.21	0.72		0.72
Unidentified fishes				0.14	0.23	0.12
Total number of prey	46	89	412	691	427	1665

Individual prey could not be enumerated

Table 4

Taxonomic composition in %O of the prey of common dolphinfish from five areas of the eastern Pacific Ocean (Fig. 1) and from all areas combined. The occurrence of hard parts (cephalopod mandibles and fish otoliths) was included. Area codes are N = north, W = west, E = east, SW = southwest, SE = southeast.

	Area					
Taxon	N	W	E	SW	SE	All
Phylum Mollusca	25.0	15.79	15.52	14.34	45.22	21.28
Class Cephalopoda	25.0	15.79	15.52	13.97	45.22	21.10
Order Teuthoidea	25.0	10.53	15.52	12.13	43.48	19.45
Family Enoploteuthidae		2.63		0.37	0.87	0.55
Abraliopsis falco		2.63		0.37	0.87	0.55
Family Mastigoteuthidae			0.86	0.74		0.55
Mastigoteuthis spp.			0.86	0.74		0.55
Family Ommastrephidae	25.0	7.89	8.62	10.29	43.48	16.88
Dosidicus gigas		7.89	6.03	7.35	37.39	13.39
Sthenoteuthis oualaniensis	25.0		4.31	2.57	8.70	4.22
Family Onychoteuthidae			9.48	1.84		2.94
Onychoteuthis banksii			9.48	1.47		2.75
Onychoteuthis spp.				0.37		0.18
Family Pholidoteuthidae				0.74		0.37
Pholidoteuthis boschmani				0.74		0.37
Family Thysanoteuthidae			0.86	0.37		0.37
Thysanoteuthis rhombus			0.86	0.37		0.37
Order Octopoda		7.89	0.86	3.68	5.22	3.67
Family Tremoctopodidae					3.48	0.73
Tremoctopus violaceus					3.48	0.73
Family Argonautidae		5.26	0.86	3.68	1.74	2.75
Argonauta spp.		5.26	0.86	3.68	1.74	2.75
Family Bolitaenidae		2.63		0.74		0.55
Japetella diaphana		2.63		0.74		0.55
Phylum Arthropoda	25.0		8.62	1.10		2.75
Class Crustacea	25.0		8.62	1.10		2.75
Order Decapoda	25.0		7.76	0.37		2.02
Family Galatheidae	25.0					0.18
Pleuroncodes planipes	25.0					0.18
Family Penaeidae			4.31			0.92
Family Portunidae			3.45			0.73
Portunus xantusii			3.45			0.73
Phylum Chordata	50.0	36.84	43.10	42.28	25.22	38.53
Class Osteichthyes	50.0	36.84	43.10	42.28	25.22	38.53
Order Clupeiformes			0.86			0.18
Family Engraulidae			0.86			0.18
Order Stomiiformes			0.86	2.21		1.28
Family Phosichthyidae			0.86	2.21		1.28
Vinciguerria lucetia			0.86	2.21		1.28
Order Myctophiformes	25.0	10.53	6.90	0.37		2.57
Family Myctophidae	25.0	10.53	6.90	0.37		2.57
Benthosema panamense		2.63				0.18

continued

Table 4 (continued)

Taxon	Area					
	N	W	E	SW	SE	All
Myctophum aurolaternatum			6.03			1.28
Myctophum nitidulum			0.86			0.18
Symbolophorus spp.		7.89	3.45	0.37		1.47
Order Lampridiformes				0.74		0.37
Family Trachipteridae				0.74		0.37
Desmodesma polystictum				0.74		0.37
Order Beloniformes	25.0	13.16	36.21	32.35	20.00	29.17
Family Belonidae			0.86		0.87	0.37
Strongylura spp.			0.86		0.87	0.37
Family Exocoetidae		13.16	25.86	28.68	19.13	24.77
Cheilopogon furcatus				0.74		0.37
Cheilopogon spilonotopterus				0.37		0.18
Cheilopogon spp.		5.26	1.72	4.04	4.35	3.67
Exocoetus monocirrhus			12.07	0.74	0.87	3.12
Exocoetus volitans		7.89	6.90	18.01	6.09	12.29
Exocoetus spp.			2.59	6.99	9.57	6.06
Hirundichthys speculiger			1.72		0.87	0.55
Prognichthys spp.			1.72	0.74		0.73
Family Hemiramphidae	25.0	2.63	24.14	6.99		8.99
Oxyporhamphus micropterus	25.0	2.63	24.14	6.99		8.99
Order Perciformes	50.0		17.24	11.40	5.22	10.83
Family Echeneidae				0.37		0.18
Rhombochirus osteochir				0.37		0.18
Family Coryphaenidae	50.0		0.86	1.84	1.74	1.83
Coryphaena equiselis	50.0			0.37		0.55
Coryphaena hippurus				0.74		0.37
Family Carangidae			1.72	1.84		1.28
Naucrates ductor			1.72	1.47		1.10
Family Gempylidae			7.76	1.47	0.87	2.57
Gempylus serpens			7.76	1.47	0.87	2.57
Family Scombridae			5.17	4.41	2.61	3.85
Acanthocybium solandri			0.86			0.18
Auxis spp.			2.59	4.04		2.57
Euthynnus lineatus			0.86			0.18
Thunnus spp.			0.86	0.37	2.61	0.92
Family Nomeidae			6.90	1.84		2.39
Cubiceps pauciradiatus			6.90	1.84		2.39
Order Tetraodontiformes	25.0	18.42	3.45	1.47		2.94
Family Balistidae	25.0	5.26				0.55
Xantichthys mento		5.26				0.37
Family Ostraciidae		10.53				0.73
Lactoria diaphanum		10.53				0.73
Family Tetraodontidae	25.0	2.63	3.45	1.47		1.83
Lagocephalus lagocephalus	25.0	2.63	3.45	1.47		1.83
Unidentified fishes				0.74	0.87	1.10
Total number of samples	4	38	116	272	115	545

08:34 hours; 13 fish had stomachs with undigested food remains, 23 had stomachs that were empty, and 2 had stomachs that contained only trace amounts of hard parts. One of the two dolphinfish in the 651–800 mm size group contained remains of flyingfishes and the other contained tetraodontid puffers. In the larger group (801–950 mm), 11 dolphinfish ate mostly triggerfishes (Balistidae), boxfish (Ostraciidae), and flyingfishes. In addition, 3 fish ≤650 mm and 2 fish in the 951–1100 mm class had empty stomachs or contained only trace amounts of hard parts.

Diel feeding periodicity

Although common dolphinfish are thought to be visual predators that feed primarily in the daytime (Massutí et al., 1998), our data suggest that they also feed at night. In the areas where sufficient sample sizes were obtained (east, southwest, and southeast), an average of about 15% of the dolphinfish caught in the early morning contained food classified in the "previous-high" category (Fig. 3). Many of these prey were flyingfishes, cephalopods, dolphinfishes, wahoo, and snake mackerel in digestion states 3 or 4 and were found in stomachs that were over 50% full. Prey of these or similar taxa were found to be completely evacuated from the stomachs of yellowfin tuna in about 6–18 h (Olson and Boggs, 1986). If dolphinfish gastric evacuation rates are on the order of those of yellowfin tuna (see "Discussion," and "Consumption rates" sections), these prey would have been ingested during the night.

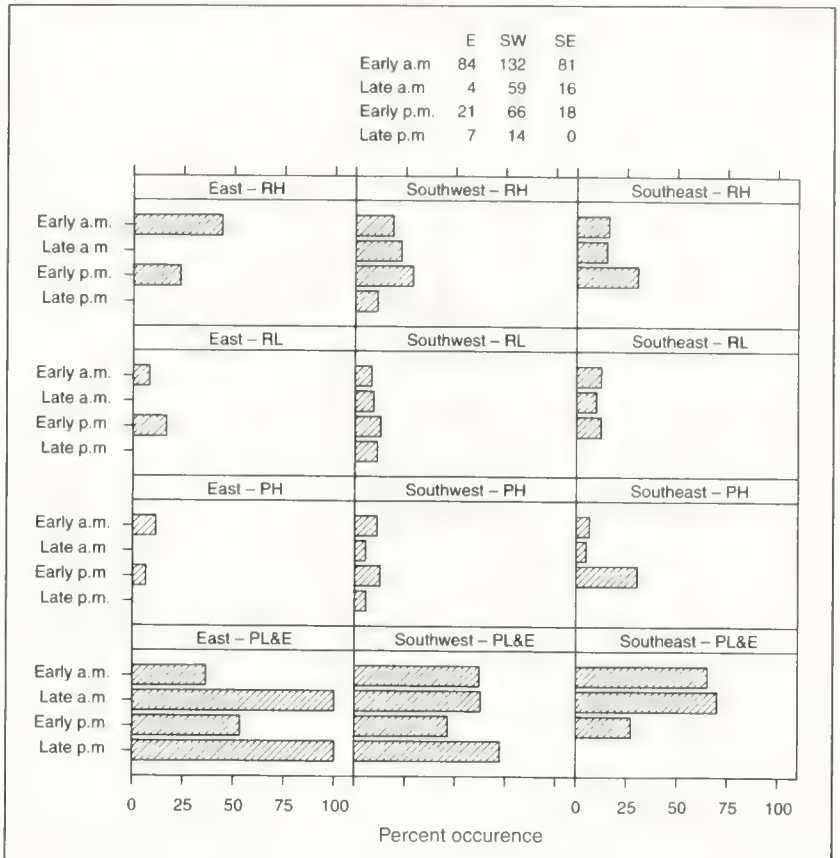

Figure 3

Percent occurrence of the prey items of common dolphinfish corresponding to four fullness-digestion categories (defined in Fig. 2) in three areas of the eastern Pacific Ocean (Fig. 1) and by the time of day the sets were made. RH = recent high, RL = recent low, PH = previous high, PL&E = previous low and empty. Early a.m. = 05:12–09:00, Late a.m. = 09:01–12:00, Early p.m. = 12:01–15:00, Late p.m. = 15:01–18:16 hours. Sample sizes for each time-area stratum are shown at the top. Data for the north area are not shown because the sample size was too small, nor for the west area because only one time stratum was represented.

We examined the time of day that the dolphinfish fed, by area. In the east area, the data indicated peak feeding activity in the early morning and early afternoon, although few samples were obtained in the late morning and late afternoon (Fig. 3, "recent high"). The most important prey taxa by percent biomass in the early morning were flyingfishes (54%), snake mackerel (Gempylidae, 18%), and epipelagic cephalopods (10%). The most important prey taxa in the early afternoon were frigate or bullet tunas (*Auxis* spp., 37%) (or a combination of both), pelagic portunid crabs (27%), and *Thunnus* spp. (yellowfin and bigeye tunas, 15%).

In the southwest area, feeding appears to have occurred throughout the day (Fig. 3). The frequency of observations in the two "recent" categories combined was highest in the early afternoon (41%) and lowest in the late afternoon (22%). The highest proportion of empty stomachs and those containing only residual hard parts occurred in the late afternoon, followed by the early and late morning. The flyingfishes dominated in the diet between 09:00 and 15:00 hours (64% and 57% by weight), and 71% of the diet of dolphinfish caught in the late afternoon was epipelagic cephalopods. The important prey in the early morning were more varied and comprised frigate and bullet tunas (*Auxis* spp., 28%), flyingfishes (18%), epipelagic cephalopods (17%), and mesopelagic fishes (primarily *Vinciguerria lucetia*, 15%).

In the southeast area, although no samples were obtained in the late afternoon, the data suggested peak feeding activity in the early afternoon (Fig. 3). The frequency of observations in both "recent" categories in the early afternoon summed to 42% of the total, compared with only 25% in the late morning. Most of the empty stomachs were from fish captured in sets made before noon. The epipelagic cephalopod *Dosidicus gigas* dominated in the diet during all time periods. Fifteen percent of the stomach contents of the common dolphinfish caught before 09:00 hours were small yellowfin tuna.

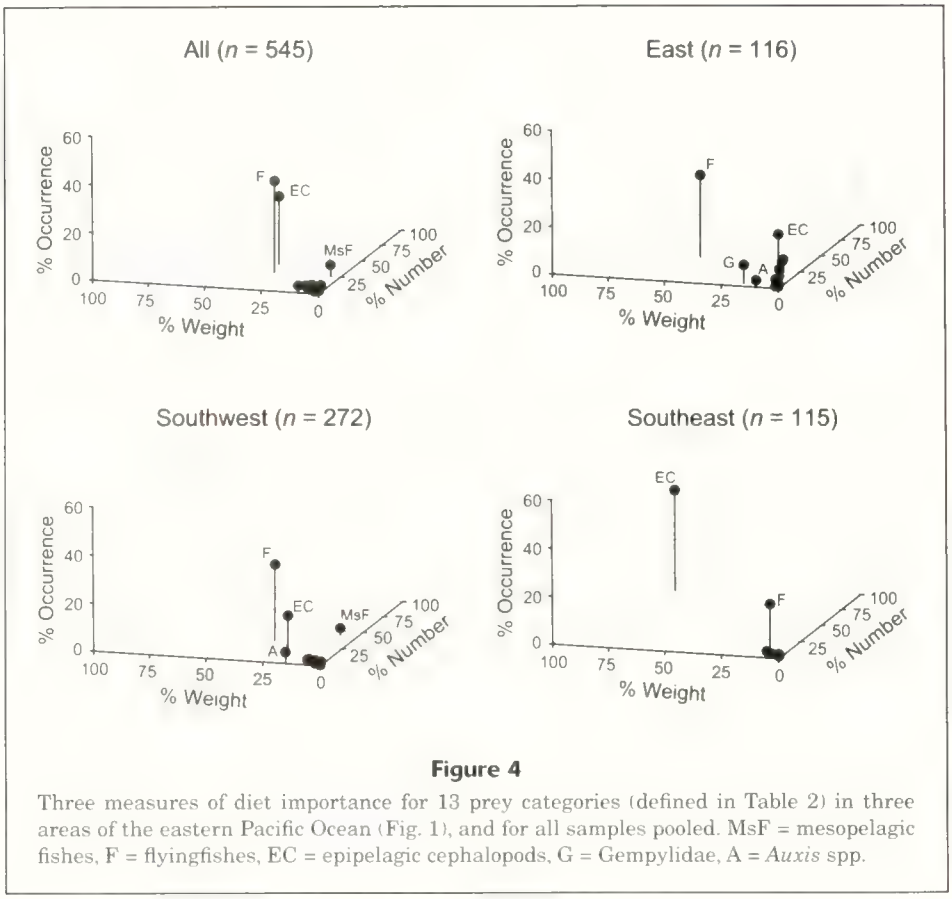

Figure 4

Three measures of diet importance for 13 prey categories (defined in Table 2) in three areas of the eastern Pacific Ocean (Fig. 1), and for all samples pooled. MsF = mesopelagic fishes, F = flyingfishes, EC = epipelagic cephalopods, G = Gempylidae, A = *Auxis* spp.

Diet measures by area

We present three measures of diet importance, $\%W$, $\%N$, and $\%O$, in Figure 4 for all samples pooled, and by area. We included the data for trace quantities of hard parts (cephalopod mandibles and fish otoliths) in the analysis of $\%N$ and $\%O$, but not of $\%W$.

The graphical representation indicates that, when all data are pooled, most components of the diet appear to be quite rare (close to the origin of the graph, Fig. 4, all). However, when the data are examined by area, the diet proves to be more varied. Flyingfishes and epipelagic cephalopods were clearly the dominant prey. Overall, flyingfishes were eaten by more of the dolphinfish (29% occurrence) than any other category, followed by epipelagic cephalopods (21% occurrence). Because 274 stomach samples were totally empty, these are equivalent to 58% and 42% occurrence, respectively, in the stomachs that contained food or hard parts. Prey counts contributed more than prey biomass to the apparent importance of mesopelagic fishes and epipelagic cephalopods in the diet. This is partly due to the accumulation of digestion-resistant hard parts of these two taxa in the stomachs.

Area was an important source of variation in the $\%W$ of three prey groups. The regression tree for epipelagic cephalopods indicated that 25% of the apparent variation in the $\%W$ of that prey was explained by area (southeast vs. others). Area was also an important predictor of flyingfish predation; 15% of the apparent variation in the $\%W$ was explained by area (north, west, and southeast vs. other areas). The regression tree for Tetraodontiformes indicated that 41% of the apparent variation in predation on that taxon was explained by area (west *vs.* others). The gravimetric importance of the 10 other prey taxa could not be modeled by regression trees (i.e. the trees pruned back to the overall mean $\%W$ for those prey) owing to their infrequency in the diet or low sample size (or to both). Nevertheless, we present our results by area to illustrate the substantial spatial variability of the diet of common dolphinfish in the EPO.

In the east area, the stomachs of 116 common dolphinfish were sampled from 1 dolphin set and 22 floating-object sets. Sixty-two of these stomachs were empty and 2 contained only trace hard parts (58.0% of the females, 52.5% of the males). The flyingfishes were the dominant prey in the east area in terms of all three indices (Fig. 4, east). Flyingfishes were eaten by 35% of the dolphinfish sampled and comprised 49% of the total weight of the stomach contents. Epipelagic cephalopods were also eaten by substantial numbers of dolphinfish (16% occurrence), and accounted for 24% of the prey counts. The epipelagic cephalopods were numerically important, but less so by weight, because their mandibles resist digestion and may accumulate in the stomachs over time. The other prey taxa were fairly rare in the east area.

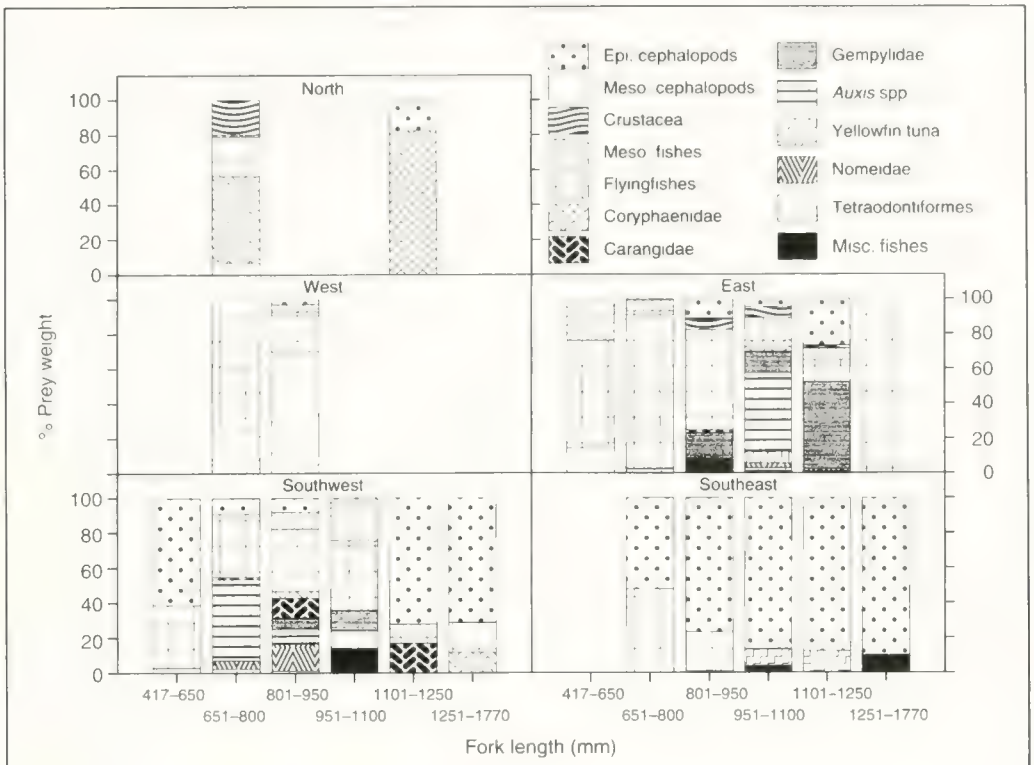

Figure 5

Gravimetric composition of prey groups (defined in Table 2), excluding trace quantities of hard parts, in the stomachs of 545 common dolphinfish sampled in five areas of the eastern Pacific Ocean (Fig. 1) versus dolphinfish size. Sample sizes for each size-area stratum are given in Table 1.

In the southwest area, the stomachs of 272 common dolphinfish were sampled from 2 dolphin sets, 5 schoolfish sets, and 22 floating-object sets. One hundred and thirty-six of the samples were empty and 14 contained only trace hard parts (60.1% of the females, 47.6% of the males). Flyingfishes and epipelagic cephalopods were found in 32% and 14% of the dolphinfish sampled, and also ranked first and second in biomass, respectively (Fig. 4, southwest). The dietary importance of both, as well as *Auxis* spp., was determined more by weight than by numbers of individuals, whereas the contrary was true for mesopelagic fishes. All the other prey categories were relatively rare in the diet according to all three measures.

In the southeast area, the stomachs of 115 dolphinfish were sampled from 1 schoolfish set and 13 floating-object sets. Fifty-two of the stomachs were empty and 7 contained only trace hard parts (44.6% of the females, 61.5% of the males). The epipelagic cephalopods were, by far, the dominant component in the diet in this area (Fig. 4, southeast). They were present in 45% of the stomachs sampled. Biomass and counts contributed about equally to the overall importance of epipelagic cephalopods in the diet. Flyingfishes also occurred in many of the samples (19%), but their contribution to the diet by weight and numbers was overshadowed by the epipelagic cephalopods. Four other diet categories were rare.

Size-specific predation

We present the prey composition in %*W*, excluding trace quantities of hard parts (cephalopod mandibles and fish otoliths), by six dolphinfish size strata for five areas (Fig. 5). Sample sizes for each stratum are given in Table 1.

Considerable variability in the diet was apparent for common dolphinfish of different sizes. However, the statistical importance of size could be detected by the regression trees for only two prey groups because of the rarity of the other prey in the diet or because of small sample sizes. The regression tree for flyingfishes indicated that 7% of the apparent variation in the %*W* of these prey was explained by dolphinfish size. Size was also an important predictor of predation on Tetraodontiformes, explaining 9% of the apparent variation in the %*W* of these prey. Although dolphinfish size was not an important predictor of predation on the other prey categories, we present the feeding data by size strata within each area because we believe this variability is biologically important.

In the east area, the flyingfishes were the most important prey group overall for dolphinfish of the three smallest size classes and of the largest size class. For the two size classes between 951 and 1250 mm, frigate and bullet tuna (*Auxis* spp.), snake mackerels (Gempylidae), and epipelagic cephalopods were dominant (Fig. 5, east).

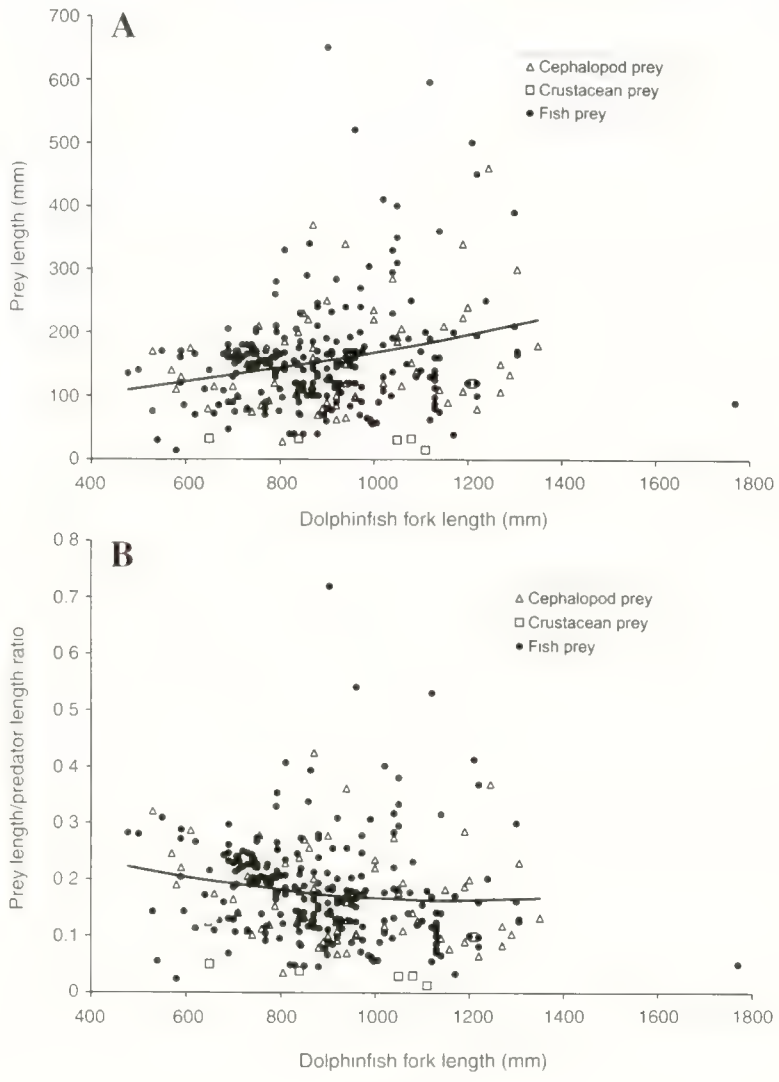

Figure 6

The length or maximum dimension of the prey (**A**) and prey relative sizes (**B**) versus dolphinfish size for three prey groups found in the stomach contents of common dolphinfish in the eastern Pacific Ocean. The lines represent the data smoothed with a smoothing spline, excluding the point for the largest dolphinfish.

In the southwest area, few large common dolphinfish were sampled (Table 1). The flyingfishes were important prey for the four smallest size groups (up to 1100 mm). Epipelagic cephalopods were important for the smallest and two largest size groups. *Auxis* spp. represented over 46% of the diet of dolphinfish between 651 and 800 mm fork length (Fig. 5, southwest).

In the southeast area, the epipelagic cephalopods dominated the diet (52–90%) of dolphinfish of all five size strata (Fig. 5, southeast). The flyingfishes comprised most of the remaining prey composition in the 651–800 and 801–950 mm categories, and *Thunnus* spp. (assumed to be mostly yellowfin tuna) comprised most of the remaining in the 951–1100 and 1101–1250 mm categories.

Prey size

We present the sizes of cephalopod, crustacean, and fish prey found in the dolphinfish stomach contents in Figure 6A. Intact prey ranged from 14 to 650 mm in length, and averaged 160 mm overall. The data smoothed with a smoothing spline showed an increasing trend of prey size with dolphinfish size. The maximum prey sizes increased gradually for dolphinfish up to about 760 mm, then abruptly to a maximum of about 600 mm for dolphinfish of approximately 1000 mm. This pattern was largely consistent for fish and cephalopod prey. Crustacean prey were small, but were consumed by a wide size range of dolphinfish.

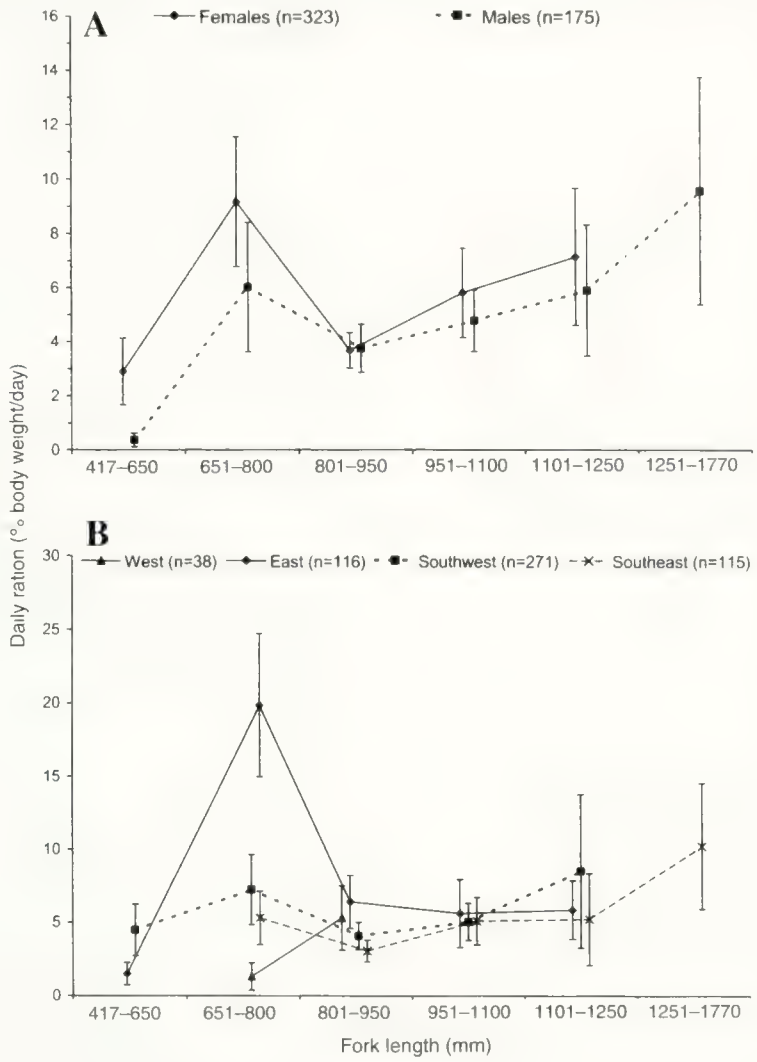

Figure 7

Mean (±1 SE) daily rations for six size strata of common dolphinfish, for all samples pooled by sex (**A**) and by area (**B**). Sample sizes are given in Table 1. Rations for some strata were not plotted if sample sizes were small (i.e. $n<5$).

The ratios of prey length to predator length ranged from 0.014 to 0.720, and averaged 0.177 (Fig. 6B). The length ratios, smoothed with a smoothing spline, showed a slight decreasing trend with dolphinfish size.

Consumption rates

The values of A_i (Eq. 1) chosen for the various prey taxa are listed in Table 2. We estimated a daily ration of 5.6 ±0.56% (mean ±1SE) of body weight per day for all common dolphinfish samples pooled. Mean ration estimates stratified by sex ranged from 0.4% of body weight per day for males of the smallest size group to 9.6% for males of the largest size group (Fig. 7A). Except for the 801–950 mm stratum, mean rations increased with dolphinfish size. Ration estimates were comparable for females and males, except for those in the smallest size stratum. The estimate for females in the 1251–1700 mm class was excluded from Figure 7A owing to a low sample size (n=2).

We present mean (±1 SE) daily ration estimates stratified by area in Figure 7B, if sample sizes were five fish or more. The calculations revealed that the 25 fish of the 651–800 mm group from the east area had ingested large amounts of food. These dolphinfish accounted for the high rations overall for both males and females of that size class (Fig. 7A). Except for that group and perhaps the 651–800 mm group in the west area, the ration estimates were comparable for all size classes in all areas (Fig. 7B). The number of empty stomachs did not unduly influence the consumption estimates by area. The percent of empty

stomachs (or containing only hard parts) ranged from 51% to 66% for the southeast, southwest, east, and west areas, respectively.

Discussion

Four previous studies of the food habits of common dolphinfish have been conducted in the EPO. Our results are difficult to compare meaningfully with those because they used different analytical techniques and had lower sample sizes. Larger sample sizes typically demonstrate greater trophic diversity (Manooch et al., 1983). Hida (1973) examined the stomachs of seven dolphinfish (two *C. hippurus* and five *C. equiselis*) caught at about 4°N–119°W. The largest component of the diet was flyingfishes (33%), followed by cephalopods (22%). Campos et al. (1993) sampled an unspecified number of *C. hippurus* caught off the Pacific coast of Costa Rica by experimental longline. Our results were similar to theirs in that flyingfishes was the most important component of the diet, and in both studies snake mackerel (Gempylidae) were found in the stomachs. Our samples from the east area, which encompasses the coastal waters of Costa Rica, contained more prey diversity, including mesopelagic fishes, portunid crabs, and penaeid shrimps. Campos et al. (1993) identified tuna of unknown species in the diet, and we found small amounts of predation on *Thunnus* spp. (yellowfin or bigeye tuna) in the east and southeast areas. Aguilar-Palomino et al. (1998) reported on the food habits of 500 *C. hippurus* caught by sport hook-and-line fishing in a small area at the tip of the Baja California peninsula, Mexico. They determined that the cephalopod *Dosidicus gigas* was the most important component of the diet, followed by the red crab *Pleuroncodes planipes*, a triggerfish, a flyingfish, and *Auxis* spp. Their results, however, could not be quantitatively compared with ours because they presented only the index of relative importance (IRI) (Pinkas et al., 1971), but not its three components (*%W*, *%N*, and *%O*). For example, it is impossible to determine if the apparent importance of *Dosidicus gigas* in their study was due to the presence of fresh biomass (i.e. high *%W*), the accumulation of numerous, small mandibles from previous meals (i.e. high *%N* and/or *%O*), or both. Likewise, the IRI indicated that small red crabs were important in the diet, but this index can be overly influenced by numerous small prey. We sampled only four dolphinfish in the north area near the south end of the Baja California peninsula and found some of the same prey taxa reported by Aguilar-Palomino et al. (1998). Lasso and Zapata (1999) analyzed the stomach contents of 228 *C. hippurus* using nonstandard methods. Their results were presented only by large categories, fishes, mollusks, and crustaceans.

Feeding periodicity

Our analysis of diel feeding periodicity suggests that, although common dolphinfish may be primarily visual predators (Massutí et al., 1998), they also feed at nighttime. Fish prey, such as flyingfishes, dolphinfishes, wahoo, and snake mackerel, would need to be ingested during nighttime hours to reach digestion states 3 or 4 before 09:00 hours the next morning, as we observed in our study, unless gastric evacuation rates are much faster than expected. Shcherbachev (1973) concluded from the presence of partially digested flyingfishes, myctophid fishes, and squids in the stomachs of *C. hippurus*, and crustacea in *C. equiselis* that dolphinfishes feed around the clock in the Indian Ocean. Rothschild (1964) described active feeding on flyingfishes and myctophids at night by *C. hippurus* in the central Pacific. Massutí et al. (1998) found that almost half of the stomachs of *C. hippurus* sampled at sunrise contained mesopelagic prey. Massutí et al. (1998) and Oxenford and Hunte (1999) also concluded that common dolphinfish feed at night, as well as during the day.

Our data analysis by area revealed an apparent relationship between the principal prey taxa in the diet and feeding periodicity. In the southwest and southeast areas, recently eaten cephalopods were in the stomachs throughout the daytime sampling period, although no samples were taken in the southeast in the late afternoon (Fig. 3). In contrast, in the east area the dolphinfish preyed mostly on fishes (flyingfishes, *Auxis* spp., and gempylids) that require more time than cephalopods for gastric evacuation (Olson and Boggs, 1986). In the east area, recently eaten prey were present only in the early morning and early afternoon, and the food remains in the late morning and late afternoon were in advanced stages of digestion. These results suggest that foraging activity may have been influenced by the digestibility and energy content of the available prey. Cephalopods are typically low in energy content, whereas fishes store lipids in the musculature and viscera and have higher energy densities (Cummins and Wuycheck, 1971). Grove et al. (1978), Flowerdew and Grove (1979), and Jobling (1981) demonstrated that low-energy foods are emptied from the stomach more rapidly than foods of higher caloric content. Elevated lipid content in natural organisms is thought to have a retarding effect on gastric evacuation (Fänge and Grove, 1979). In yellowfin tuna, gastric evacuation rates were inversely correlated with total lipid content of four food organisms (Olson and Boggs, 1986). Apparently, the dolphinfish in the southwest and southeast areas spent more time foraging to fulfill their energy requirements than the dolphinfish in the east area.

Diet considerations

Our study indicated that only two prey groups, flyingfishes and epipelagic cephalopods, were dominant in the diet of common dolphinfish in the EPO (Fig. 4).

Diet differences we attributed to spatial stratification also had a seasonal component. Of the stomach samples obtained north of the equator in the north, west, and east areas, most (85%) of those that contained fresh food, were caught from May through November. The trends described for common dolphinfish in the southwest and southeast areas may also have been attributable to seasonality of the prey from December through April because all the dolphinfish in these areas were caught during these months.

The marked differences in food habits with predator size are noteworthy. For all areas combined, the general trend was for increased predation on cephalopods and decreased predation on flyingfishes as the dolphinfish grew larger. The exception was the smallest size group (417–650 mm). These dolphinfish ate 50% cephalopods and 40% flyingfishes by weight. Zavala-Camin (1986) also found greater predation on cephalopods by large dolphinfish (>850 mm) than by smaller specimens off Brazil.

Piscivores are known to feed selectively according to prey body size (Tonn et al., 1992). Maximum prey size is determined by the mouth gape of the predator (Magnuson and Heitz, 1971; Hambright, 1991), and minimum prey size was correlated with the gap width between the gill rakers for a variety of tunas, mackerels, and dolphinfishes (Magnuson and Heitz, 1971). Preference for the largest prey a predator can ingest is supported on theoretical grounds (Ivlev, 1961; Harper and Blake, 1988), but a survey of studies examining prey-size selectivities of piscivorous fishes showed a consistent pattern of selection for small prey (Juanes, 1994). In our study, the common dolphinfish of all sizes ingested small prey (Fig. 6A). Ratios of prey size to predator size for piscivores tend to average 0.2–0.3 (Juanes, 1994). In our study, the dolphinfish ingested prey that averaged slightly smaller, 17% of their length. A few dolphinfish ate prey that were greater than the maximum reported for piscivores, 50% of their length (Juanes, 1994).

Consumption rates

The method we employed for estimating daily rates of food consumption was judged by Cortés (1997) to be among the two most appropriate methods for top predators. However, applying gastric evacuation rates derived for yellowfin tuna to estimate daily rations of common dolphinfish requires justification. Suzuki's (1992) observations of gut-evacuation times of small dolphinfish do not unequivocally justify our assumption that gastric evacuation rates are comparable to those of yellowfin tuna, which were based on food passage through the stomach alone. However, energetics requirements suggest that gastric evacuation times for dolphinfish, at the same temperature, would be on the order of those for yellowfin. Our hypothesis is supported by the similar standard metabolic rates of common dolphinfish and yellowfin (Benetti et al., 1995; Brill, 1996). Brill (1996) argued that high rates of digestion are consistent for high-performance fishes like tunas, billfishes, and dolphinfishes and demonstrated that dolphinfishes share several characteristics of high-performance physiology with tunas and billfishes. Other, similar-size teleost fishes require about five times as long as yellowfin and skipjack to evacuate a meal (Magnuson, 1969; Olson and Boggs, 1986). Until gastric evacuation rates of dolphinfish are measured, we are confident that our first-order estimates are adequate approximations of daily rations of common dolphinfish in nature.

Our ration estimates for common dolphinfish are greater than those for yellowfin tuna of comparable size, estimated by the same method (Olson and Boggs, 1986; Olson and Mullen, 1986). Our estimates are consistent with the observation that, although standard metabolic rates and locomotion costs are comparable for these species, common dolphinfish have greater growth rates than yellowfin (Uchiyama et al., 1986; Wild, 1986) and may require more energy for growth.

In summary, dolphinfish are an important component of the pelagic food web in the EPO, and as such, their feeding ecology provides clues to the underlying ecosystem structure. Clearly, *C. hippurus* imparts predation pressure on cephalopods, flyingfishes, and other prey that are shared by a suite of predators (Juhl, 1955; King and Ikehara, 1956; Blunt, 1960; Perrin et al., 1973; Nakamura, 1985; Olson and Boggs, 1986; Robertson and Chivers, 1997; Markaida and Sosa-Nishizaki, 1998). This predation pressure lends support to the hypothesis that cephalopods and flyingfishes are abundant or have high ratios of production to biomass (P/B) (or both) in the EPO. This hypothesis is based on 1) high consumption rates on these prey, indicated by the stomach contents in our present study, 2) high P/B of dolphinfish (Oxenford, 1999), 3) high consumption rates of cephalopods and flyingfishes by other predators (cited above), and 4) high P/B of those predators (Boggs, 1989; IATTC, 1999). This analysis illustrates the importance of diet studies for providing ecological insights.

Our study provides key data for implementing ecosystem analyses based on food-web models (Christensen and Pauly, 1992; Walters et al., 1997). For example, *Ecopath with Ecosim* (www.ecopath.org) requires data on both the diet compositions and consumption rates of predators. Accordingly, we summarized the prey data by several levels of taxonomic resolution and functional groups for dolphinfish sampled at multiple spatial scales and size classes. These data help lay the groundwork for a community- and ecosystem-level approach to fisheries management in the EPO.

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Recruitment season, size, and age of young American eels (*Anguilla rostrata*) entering an estuary near Beaufort, North Carolina

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Abstract—Net catches from 1985–86 to 1994–95 at Pivers Island, North Carolina, indicated that glass-eel stage American eels (*Anguilla rostrata*) were recruited to the estuary from November to early May, with peak numbers in January, February, and March. There was no declining trend in recruitment over the years of sampling. Except for one year, there was no clear seasonal decrease in mean length. But shorter glass eels were older than longer glass eels, as judged by age within the glass eel growth zone of the otolith, suggesting that smaller fish took longer to arrive. The mean age of glass eels collected from the lower estuary and a freshwater site 9.5 km upriver differed by 8.4 d (36.2 vs. 44.6, respectively). Outer increments (30–35) of the otolith growth zone of glass eels from North Carolina were significantly wider than corresponding increments of otoliths from New Brunswick. Mean total ages of North Carolina, New Jersey, and New Brunswick elvers were 175.4, 201.2, and 209.3 d, corresponding to mean lengths of 55.9, 60.9, and 58.1 mm TL, respectively. The mean durations of glass-eel growth zones (44.6, 62.3, and 69.8) were in close agreement with those from previous studies, but total ages were not. This suggested that perhaps some finer (leptocephalus stage) increments were not detected by light microscopy, differences occurred in seasonal increment deposition, or absorption of the otolith material may have taken place during metamorphosis, rendering the aging of larvae inaccurate. Judging from the long recruitment period and seasonal uniformity in both mean age and length found in our study, the spawning period of American eels may be somewhat more protracted than previously considered.

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The life history of the American eel (*Anguilla rostrata*) is both fascinating and mysterious. It spawns in the Sargasso Sea and the young willow leaf-shaped leptocephalus larva disperses over great distances before it metamorphoses into a transparent glass eel. This stage reaches the estuaries of North America where it typically ascends rivers and streams as an elver, becoming progressively more pigmented as the run progresses. This stage is followed by the juvenile or yellow eel, and finally by the silver or maturing adult (Able and Fahay, 1998). Eel physiology and ecology are still not completely understood, although much has been learned since the early 1900s. Schmidt (1922) discovered the general area of spawning in the Sargasso Sea, and Kleckner et al. (1983) further demarcated breeding to an area defined by thermal front boundaries. Comparini and Rodino (1982) used electrophoretic analysis on American and European eel (*Anguilla anguilla*) leptocephali to confirm that both spawn in the Sargasso Sea.

Based on oceanographic surveys and entrance times into rivers, estimates of migration time to North America of young *A. rostrata* range from 250 days to one year, corresponding with a peak spawning time of February and March (McCleave et al., 1987; Haro and Kreuger, 1988). Many studies have described seasonal sizes of European glass eels and elvers entering estuaries, but similar long-term data sets for the American species are uncommon. Elvers enter estuaries along the coast of North America progressively from south to north, becoming larger with increasing latitude (Haro and Kreuger, 1988), and for many (but not all) areas, sizes have been recorded. We document the recruitment period and variations in its seasonality for the Beaufort, NC, region for the 1985–86 to 1994–95 seasons.

Michaud et al. (1988) documented the sizes but not the ages of American eel elvers entering a Quebec river. Jessop (1998) used large samples from the Nova Scotian elver fishery to show seasonal declines in length and weight and an increase in pigmentation of newly arrived elvers. Wang and Tzeng (1998) used SEM (scanning electron microscopy) and elemental analysis of otoliths to determine ages of elvers taken from Haiti, north to Nova Scotia. They also estimated the length in days of the leptocephalus and glass-eel stages from the same sites. Helfman et al., (1984) described the length range of glass eels entering a Georgia river in February. Although most earlier workers (e.g. Vladykov, 1966; Eldred, 1968, and others) did not have long-term data series, their samples are useful for comparisons with current data.

Long-term records of estuarine recruitment of early life-history stages of eels are particularly relevant at this time, when reduction in juveniles (but not elvers) to the upper St. Lawrence River area in North America has been noted (Castonguay et al., 1994a), and when catches of adults and recruitment of elvers are declining in Europe (Castonguay et al., 1994b). We therefore present subsamples of ages along with our catch per effort (densities) for glass eels. Earlier studies of eel otoliths used SEM to determine ages, but we used light microscopy for comparison with such studies. Castonguay (1986) aged *A. rostrata* leptocephali captured in the Gulf of Maine, and his largest individual of 49 mm TL (which would shrink during metamorphosis) was 130 d. However, only the daily growth increments in the elver growth zone (area after the "transition" or "elver" check) have been validated (Martin, 1995). He validated daily increments in the field over a one-month period. Lecomte-Finiger (1992) aged otoliths of *A. anguilla* elvers from several European locations, as did Antunes and Tesch (1997). The latter suggested that daily increments of *A. anguilla* may be underestimated because of the "diffuse" (their term) nature of the metamorphosis zone. More recently, Cieri and McCleave (2000) suggested that there are a number of inconsistencies when growth zones of leptocephali are compared with the same zone in the otoliths of glass eels and juvenile American eels. Both radii and ages were less in the older fish stages than in the leptocephali. The possibility of resorption of otolith material during metamorphosis (and subsequent obliteration of increments) led them to discourage the use of larval eel otoliths for aging or back-calculating life history events until these discrepancies could be explained. Although the present authors could not validate increments in the leptocephalus stage or metamorphosis stage (these stages metamorphose before reaching North Carolina), we collected samples to temporally validate daily increments in the glass-eel stage. We tested the hypotheses that 1) the increment number for glass eels at an upriver (freshwater) location would be greater than that for glass eels at a lower (estuarine) sampling site by a difference (in days) equal to the distance divided by the sum of the swimming speed and tidal transport, and that 2) increment widths for corresponding glass-eel portions of the otolith for fish from the Bay of Fundy (New Brunswick sample) would be narrower than for fish of warmer water (i.e. North Carolina) because the warmer waters would produce faster growth which, in turn, could produce wider otolith increments. A New Jersey sample was also aged to represent an intermediate geographic position between North Carolina and New Brunswick.

The objectives of this study were 1) to describe the 1985–95 annual recruitment of glass eels to the estuary near Beaufort; 2) to present the variations in seasonal densities of glass eels; 3) to analyze the seasonal length frequency by weekly intervals, and 4) to compare mean ages of glass eels at three locations along the eastern coast of North America (North Carolina, New Jersey, and New Brunswick). We also tested two hypotheses relevant to validating daily deposition of otolith growth increments in the glass-eel stage of *Anguilla rostrata*.

Methods

Collections

Glass eels were collected from two sites in North Carolina: 1) in the lower Newport River at Pivers Island, about 2 km inside Beaufort Inlet; and 2) at Black Creek, a small tributary of the Newport River, at the entrance to a millpond, about 9.5 km upriver from Beaufort, North Carolina. The samples at Pivers Island were collected over the 10-year period 1985–95 with a 1×2 m neuston net fitted with 945-um mesh and flow meter and suspended from a bridge, except during 1985–86, when 60-cm bongo nets were used. Details of the sampling protocol are given in Warlen (1994). Samples were always collected at night during midflood tide, from November to April. Density of fish in the catches was standardized as the mean number per 100 m^3. Additional samples were collected by dip net from Black Creek just below a small dam leading into a millpond (22 February and 20 March 1994). Samples were also obtained from two areas north of North Carolina: 1) Little Egg Inlet, New Jersey, at the site of the Marine Field Station, State University of New Jersey, Rutgers,Tuckerton, NJ (39°30′N, 74°14′W) on 21 Februrary and 9 March 1994 (with a 1-m plankton net); 2) elvers were captured from the Lepreau River, at the village of Lepreau, New Brunswick, Canada, on the Bay of Fundy (45°00′N, 66°20′W) on 6 June 1994. This sample was collected with a 1-mm mesh dip net and was preserved in 70% ethanol. All other samples were preserved in 95% ethanol, and then preserved in fresh 70% ethanol after 24 h.

Aging methods

All eels were measured (TL to the nearest 0.1 mm) with a Vernier caliper and saggital otoliths were removed, washed, dried, and mounted on glass slides with thermal cement, sulcus groove down. The otoliths were ground with a series of wet grit papers (no. 600 to 1200) until the core was visible, then polished with diamond paste, after which they were aged by using an oil-immersion lens from 1200 to 3100×. A subsample of 10 otoliths was also sectioned (transverse) and prepared for reading, and ages were compared with ages from whole otoliths from the same fish. Sectioned otoliths had about 4% more rings in the outer edge. Otolith increments were read from the hatching ring outwards, as suggested by Lecomte-Finiger (1992) and Tzeng (1996). Umezawa and Tsukamoto (1991) found that no rings were formed during the incubation period (5 days) of *A. japonica*. To maintain consistency with other authors, we therefore added five days to our ages. An optical imaging system was used to count increments and to measure increment widths and the distance from the core to the first-feeding (exogenous) ring, etc. The lowest increment width (distance between adjacent dark rings) recorded was 0.326 µ, a distance which was probably close to the resolution minimum of our microscope. Incremental counts were made of the leptocephalus growth zone, the metamorphic zone, the glass-eel growth

zone, and from the "elver" check (transition mark) to the edge of the otolith (see Cieri and McCleave, 2000). Total ages were estimated as the age from the hatching ring to the elver mark. Glass-eel growth zone ages (increments from the outer boundary of metamorphic zone to elver check) were read as in Wang and Tzeng (1998).

Age studies

The mean ages in the glass-eel growth zones of eels taken at Pivers Island in February were compared with mean ages in glass-eel growth zones of eels taken at an upper estuary site, the Black Creek Mill Pond entrance (also in February). The difference in mean age presumably reflected the time required to travel the distance upriver to the collection site.

The total ages and the ages found in the glass-eel growth zone were compared with those for small and larger glass eels arriving during the recruitment season. Glass eels were divided into length groups (from 46.1–48.0 TL to 58.1–60.0) and corresponding age frequencies were assigned to each length group. A linear regression was then fitted to the data to assess whether or not smaller fish were older or younger than the longer members of their recruitment class.

Statistical analysis

Seasonal trends in the weekly length distributions were examined by linear regression (SAS Institute, 1996) for each sampling (recruitment) season, and for the whole 10-year period (1985–86 to 1994–95).

The differences in otolith increment widths in the early (proximal) glass-eel growth zone (increments 10–15) and later (mid-distal) glass-eel growth zone (increments 30–35) from the New Brunswick and North Carolina samples were examined by analysis of variance (ANOVA). Age distributions of glass eels captured by month were compared by using the *F*-test. Statistical significance was accepted at $P < 0.05$.

Results

Annual recruitment

The total density of glass eels in the Beaufort estuary varied considerably between 1985 and 1995, but there was no significant trend (F_8=1.605, adj r^2=0.123, slope=–0.031, P=0.246) among the 10 consecutive recruitment years in the Beaufort estuary (Fig. 1). Densities were highest in 1988–89 and 1993–94 (13.5–14.0 eels/100 m^3) and lowest in 1990–91 (1.5 eels/100 m^3), a ninefold difference. Apart from the low of 1990–91, all other years had total densities of more than seven eels/100 m^3. After the 1990–91 low, the total annual density of elvers at Beaufort increased again (F_3=4.88; slope 2.04, r^2=0.78, P=0.113), approaching the previous mean level.

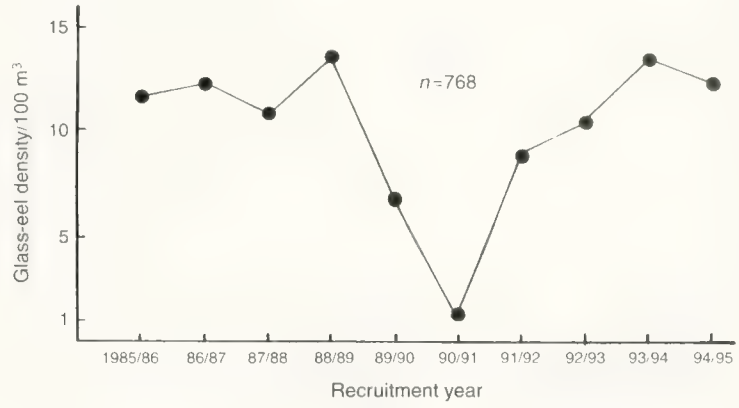

Figure 1

Mean density of *Anguilla rostrata* glass eels (no. of eels/100 m^3) caught each year, from 1985–86 to 1994–95, between November and April at Pivers Island, Beaufort, North Carolina.

Seasonal recruitment

Although glass eel recruitment sometimes occurred over a 5 1/2 month period (mid-November to early May), most recruitment of young eels to the estuary occurred from December through April (Fig. 2). Although there was some variation among years within the recruitment period, the largest catches usually occurred in February and March. Peak catches varied from early in the season (1985–86) to late in the season (1987–88). In 1993–94, densities were highest in mid-January and mid-March. In (1990–91), the year with the lowest catches, almost all of the catch occurred in December and January, with virtually none afterwards.

When seasonal changes in length of glass eels among recruitment years were analyzed (Table 1), the slope of the regression for all 10 years (Fig. 3) was positive, but not significant (F_1=19.50, P=0.001). Four seasons had negative regression slopes and slopes for the other years were positive, three of which were significant.

Age studies

The mean age observed in the glass-eel growth zones of eels collected in February from the Pivers Island and Black Creek sites differed significantly, by eight days (F_2= 6.651, P=0.003). The Pivers Island eels averaged 36.2 d (52.9 ±0.9 mm TL) for their as yet uncompleted glass-eel phase, and the Black Creek elvers averaged 44.6 d (55.9 ±0.9 mm TL). The distance between the two sites was about 9.5 km.

In respect to otolith growth, the mean widths of the first 10–15 daily growth increments in the glass-eel growth zone (Table 2) were not significantly different (F_2=1.363, P=0.185) between the northern eels (New Brunswick) and the southern eels (North Carolina). However, both samples of otoliths from North Carolina indicated that mean

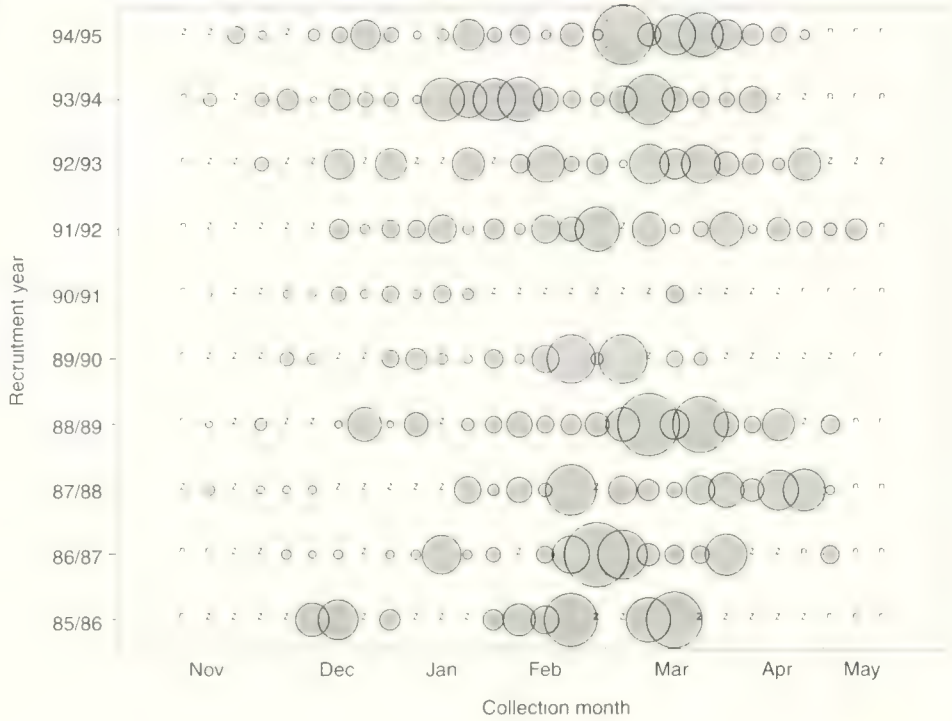

Figure 2

Total densities of *Anguilla rostrata* glass eels (no. of eels/100 m^3) by week during recruitment seasons, from 1985–86 to 1994–95. Larval density is proportional to circle area: smallest density (0.034) at week 2 of season 1990–91; largest density (3.690) at week 17 of 1986–87 season. n = no sampling and z = sampling with zero catch.

Table 1

Linear regression coefficients for total length on collection week for glass-eel stages of American eel taken at Pivers Island, Beaufort, North Carolina, in each of 10 recruitment seasons, with 95% confidence intervals for slopes and intercepts. P is the probability of failing to reject the H_0 All years: $Y = 52.15 + 0.088X$ (r^2=0.026).

Recruitment year	n	Adjusted r^2	Intercept	Slope	F	P
1985–86	34	0.19	48.92 ±3.48	0.24 ±0.15	1.58	0.245
1986–87	61	0.03	50.87 ±2.94	0.15 ±0.14	2.87	0.095
1987–88	73	0.11	50.63 ±2.49	0.19 ±0.12	10.21	0.002
1988–89	81	0.02	52.65 ±2.41	0.09 ±0.07	2.27	0.136
1989–90	48	0.00	54.45 ±2.80	–0.09 ±0.08	1.03	0.315
1990–91	15	0.07	53.18 ±5.24	–0.01±0.39	0.00	0.958
1991–92	60	0.33	48.82 ±1.70	0.27 ±0.10	30.66	0.001
1992–93	60	0.01	54.11 ±4.00	–0.07 ±0.07	1.37	0.247
1993–94	18	0.02	54.94 ±1.48	–0.09 ±0.09	3.70	0.057
1994–95	132	0.01	52.97 ±1.55	0.07 ±0.08	2.40	0.124

incremental widths (1.717 and 1.732) in the later stage of the glass eel (increments 30–35), were wider (F_2=3.93 , P=0.004) than the corresponding mean width (1.314) for New Brunswick otoliths, as hypothesized, suggesting faster growth in the southern waters.

The youngest (mean 168 d) American eel elvers were found at the Pivers Island site (Table 3), whereas elvers at Black Creek (just north of Pivers Island) were not significantly different at age 175 d (F_2=1.125, P=0.376). Neither elvers from New Jersey (201 d) nor those from New

Table 2

Mean increment widths (microns) with 95% confidence limits in the glass-eel growth zone of *Anguilla rostrata* otoliths from three different sampling sites and the number showing the "elver" or "transition" mark. Number in sample (n) applies to both increment groups. Means without a letter in common (y and z) were significantly different ($P \leq 0.05$).

Sample site	n	Width (μ) of 10–15th increment	Width (μ) of 30–35th increment	Presence of elver mark (%)
Pivers Island, North Carolina	77	1.425 ±0.114 z	1.717 ±0.189 z	0
Black Creek, North Carolina	27	1.330 ± 0.169 z	1.732 ±0.180 z	93
Lepreau, New Brunswick	43	1.232 ±0.168 z	1.341 ±0.163 y	98

Table 3

Means (±SD) for total age, glass-eel age, and total length (TL) for young eels, *Anguilla rostrata* collected in our study. Only glass-eel ages were significantly different (*) between locations (F-test, $P \leq 0.05$). n = number of otoliths analyzed.

Location	Date	n	Total age (d)	Glass eel age (d)	Length (TL mm)
Pivers Island, North Carolina	Dec–Apr 1985–94	77	167.2 ±16.9	36.2 ±3.2*	52.9 ±2.4
Black Creek, North Carolina	2–23 Feb 1994	25	175.4 ±12.6	44.6 ±1.6*	55.9 ±3.1
Little Egg Inlet, New Jersey	Feb–Mar 1994	22	201.2±16.1	62.3 ±8.8*	60.9 ±3.0
Lepreau, New Brunswick	6 June 1994	43	209.3±18.1	69.8 ±10.5*	58.1 ±3.8

Table 4

Regression of collection week (1–26) against total age in days (with 95% confidence limits) and regression of glass-eel growth zone age (outer metamorphic zone to elver check on otolith) against total length (mm) for glass eels collected at Pivers Island, North Carolina. The sampling period (recruitment season) extended from November to mid-May, 1985–86 to 1994–95. n = number of otoliths analyzed.

	n	Slope	Adjusted r^2	Intercept	P	Mean age
Collection week against total age	89	0.339	0.053	170.2	0.976	173.1 ±2.7
Glass eel growth zone age against total length	89	– 0.311	0.499	77.5	0.014	60.6 ±1.7

Brunswick (209 d) were significantly older than those from North Carolina (F_2=1.111, P=0.407; F_2=1.140, P=0.373) with respect to total age. Although New Jersey fish appeared to be longer (60.9 mm TL) than New Brunswick elvers (58.1 mm TL), the difference in mean length was not significant (F_2=1.283, P=0.266).

Although total mean age (d) counts were not significantly different between sites (Table 3), glass-eel age (the portion between metamorphosis zone and elver mark of otolith) differed between all three sites (NC vs. NJ, F_2= 7.713, P=0.005; NJ vs. NB, F_2=1.622, P=0.091). Furthermore, when glass-eel ages were regressed against latitude, the relationship was significant (slope=0.303, adj. r^2=0.835, P=0.028).

In light of Jessop's (1998) finding of a decrease in length over the recruitment season for elvers in the Bay of Fundy waters, we re-examined our age data by month and length. Could it be that even though our lengths showed no significant seasonal decrease, shorter fish were, on average, older than longer fish? The regression of the capture date against total mean age suggested an increase in age over time (Table 4), but the relationship was weak (adj. r^2=0.053). Furthermore, an F-test revealed no difference in incremental total age between any month. But total age is apparently not to be trusted (Cieri and McCleave, 2000). When we regressed mean length against only the glass-eel zone age, it revealed just the opposite relationship: a negative slope (Table 4), with a good relationship (adj. r^2=0.499). The smaller fish during the recruitment period were indeed older, as suggested by Jessop (1998). The longer fish, on average, had fewer increments in their glass-eel growth zone than the shorter fish, suggesting that the latter had taken longer to reach Beaufort estuary from the Sargasso Sea.

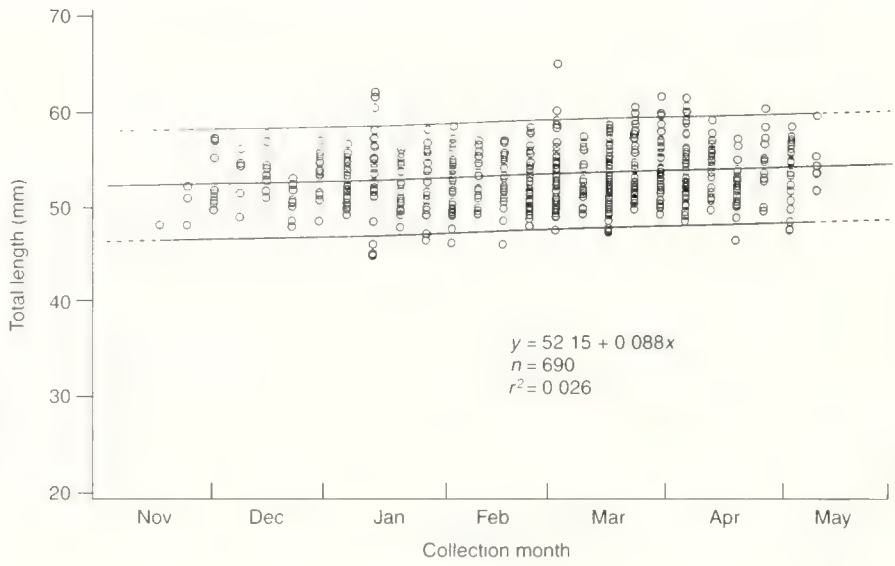

Figure 3

The regression of total length on week of capture for *Anguilla rostrata* glass eels collected at the Pivers Island bridge during 10 recruitment seasons from 1985–86 to 1994–95. Boundary lines represent 95% confidence limits.

Discussion

Glass eels were recruited to the Beaufort estuary over a 7-month period from November to early May during the ten years from 1985–86 to 1994–95. Peak recruitment occurred in February–March of most years. Catch distributions were usually skewed, either positively or negatively, and clumped. Variation in estuarine recruitment time may have been due to differences in oceanic transport rates for larvae, and perhaps to slight differences in times of peak spawning, a well-known phenomenon in many other fish species. Able and Fahay (1998) also found that most glass eels recruited to a New Jersey estuary from January to June (in 1991 to July), with peaks usually in February and March. In Nova Scotia the main fishery for elvers in 1997 extended from late April to mid-August (Jessop, 1998). The recruitment period for the two southernmost localities and Nova Scotia thus overlapped in April and May: as the North Carolina and New Jersey recruitment period ends, the northern Bay of Fundy area typically commences.

Although there was a large variation in the numbers of eels caught among years, there was no indication of an overall reduction in recruitment. Castonguay et al. (1994b), and Marcogliese et al. (1997) have suggested a number of possible reasons for a decline of European eels, but such a decline was not reflected in our catches of elvers at Beaufort. Jessop (1997) also concluded that there had not been a decline in elvers recruited to Atlantic coastal waters of the Canadian maritime provinces over the past decade (last year 1996).

The lengths of elvers captured in the tidal net at Pivers Island fell within the expected latitudinal length range reported by Haro and Kreuger (1988) and were similar to the 49–56 mm TL length range for glass eels from a river in Georgia (Helfman et al., 1984). Mixed elvers and small juveniles (not aged) in the Great Bay area of New Jersey, from 1986 to 1994 averaged 60–90 mm TL (Able and Fahay, 1998). Elvers collected by Jessop (1998) in 1997 in the Bay of Fundy waters ranged from 52.0 to 70.0 mm TL (considerable variation was evident among rivers of New Brunswick and Nova Scotia.). Even farther to the north (Quebec), Michaud et al. (1988) reported lengths of elvers for 1987 from the St. Lawrence River estuary to extend from 50 to 70 mm TL. Comparing our data with that of other studies, and allowing for 2.8% shrinkage in length of our eels (unpubl. data) due to alcohol preservation (our samples), as opposed to 1–2% shrinkage in 6–10% formalin (Jessop, 1998; Stobo, 1972), we found that there was a remarkable consistency in the clinal length ranges from north to south. Some inconsistency was expected because we compared studies in which sampling was done at both river mouths and estuaries, where it is known that ascent up rivers is usually dependent upon temperature or stream level (Martin, 1995; Jessop, 1998).

In a study of the Bay of Fundy waters, Jessop (1998) showed that as the season progressed, lengths of young eels entering most, but not all, rivers declined to a maximum of 7%. The length of recruiting European eel elvers also declined seasonally (Cantrelle, 1981). Yet our combined length-frequency plot of all fish collected over the ten-year period showed a nonsignificant regression. It may be that only elvers to the north of our location show a definitive decrease in lengths over time or that our samples were too small to confirm the phenomenon.

The difference in estimated mean age of 8 days from glass-eel growth zones at two North Carolina locations about 9.5 km apart implies that upriver movement was about 1 km a day, much of which could be tidal. We do not know whether or not this rate of movement is reasonable or typical.

The mean age from our glass-eel growth zones on otoliths of glass eels agreed with the ages determined from other glass eels collected in North Carolina (Wang and Tzeng, 1998).

Finally, the apparent total ages and glass-eel ages from North Carolina, New Jersey, and New Brunswick support the hypothesis that eels are progressively older to the north, and are consistent with their greater distance from the Sargasso Sea.

Total age estimates of glass eels can be compared with those from two other studies of American eel. Our average total age of glass eels from Black Creek (175 d) was 14% older than the 153 d that Budimawan (1996) found for the same location, date, and year. On the other hand, estimated total ages of glass eels were considerably less (20–22%) than the ages obtained by Wang and Tzeng (1998) for eels from the same general areas (but different dates). Because ages from glass-eel growth zones (as opposed to total age) were in very close agreement with those of Wang and Tzeng (1998), one assumption for this inconsistency in total age is a difference in interpreting age in either the leptocephalus or metamorphic zone. It is also possible that increments ≤0.3 µ wide may not have been distinguishable by light microscopy, which could account for our ages being younger than those of Wang and Tzeng (1998), who used SEM. Antunes and Tesch (1997) have also suggested that these two methods of otolith observation may produce different results. It is conceivable that increments in the leptocephalus growth zone may be laid down in fewer numbers in some seasons, but it seems unlikely that low water temperatures would cause a cessation of otolith increment deposition, because the Gulf Stream top 200-m layer (the assumed habitat of leptocephali) maintains an annual temperature above 16°C (Stommel, 1965). Absorption of increments during metamorphosis (Cieri and McCleave, 2000) is possible, but our studies could not shed any light on this proposed phenomenon because all leptocephali had metamorphosed before reaching North Carolina. Obviously, there is consistent agreement among authors in incremental counts of glass-eel growth zones, which are wide and clear, and therefore easy to count.

Regardless of the discrepancy in age estimates of larval eels, evidence from the rate of transport of other species in the Gulf Stream suggests that once they have reached the Gulf Stream, it is possible for leptocephali to reach the continental shelf of North Carolina in about 110 days. A NOAA (National Oceanic and Atmospheric Administration) sea drifter released in 1996 west of the western edge of the Sargasso Sea in 1996 and travelling just inside the western front of the Gulf Stream at 100 m depth reached the North Carolina outer continental shelf in 50 days. Its release site appears to overlap stations where leptocephali of *A. rostrata* were captured (Wippelhauser et al., 1985; Kleckner and McCleave, 1985). Larvae of several fish species from Florida waters are known to reach the area offshore North Carolina in 25–30 d (Hare and Ahrenholz).[1] For example, larval Atlantic menhaden (*Brevoortia tyrannus*) that spawned offshore from Beaufort in an area close to the path of the sea drifter reached the estuary near Beaufort, North Carolina, in an average of 60 d (Warlen, 1994). This estimate of across-continental shelf transport, when added to the 50 d of travel for the sea drifter, gives an elapsed time of 110 d. This estimate of transport duration may prove to be useful in the future.

McCleave et al. (1998) surmised that leptocephali of the European eel (virtually identical in physical structure to *A. rostrata*) do not actively swim toward land during their migration to Europe. Granted that the age increments in the larval zone of the otolith of American eels may not accurately depict early life-history duration (Cieri and McCleave, 2000), the consistency of recruited lengths and glass-eel ages over the years from 1985 to 1995 is noteworthy. In addition, the annual recruitment seasons and sizes observed in coastal North Carolina and New Jersey regions (Able and Fahay, 1998) reveal a remarkably consistent sequential latitudinal pattern. It appears that current data on seasonal recruitment of young eels should continue to be used to examine temporal relationships between geographical areas and oceanic transport times from the spawning area (Sargasso Sea) to the estuaries.

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Changes over time in the spatial distribution of walleye pollock (*Theragra chalcogramma*) in the Gulf of Alaska, 1984–1996

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Abstract–Triennial bottom trawl survey data from 1984 to 1996 were used to evaluate changes in the summer distribution of walleye pollock in the western and central Gulf of Alaska. Differences between several age groups of pollock were evaluated. Distribution was examined in relation to several physical characteristics, including bottom depth and distance from land. Interspecies associations were also analyzed with the Bray-Curtis clustering technique to better understand community structure. Our results indicated that although the population numbers decreased, high concentrations of pollock remained in the same areas during 1984–96. However, there was an increase in the number of stations where low-density pollock concentrations of all ages were observed, which resulted in a decrease in mean population density of pollock within the GOA region. Patterns emerging from our data suggested an alternative to MacCall's "basin hypothesis" which states that as population numbers decrease, there should be a contraction of the population range to optimal habitats.

During 1984–96 there was a concurrent precipitous decline in Steller sea lions in the Gulf of Alaska. The results of our study suggest that decreases in the mean density of adult pollock, the main food in the Steller sea lion diet, combined with slight changes in the distribution of pollock (age-1 pollock in particular) in the mid-1980s, may have contributed to decreased foraging efficiency in Steller sea lions. Our results support the prevailing conceptual model for pollock ontogeny, although there is evidence that substantial spawning may also occur outside of Shelikof Strait.

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The incorporation of space into ecological models has increased our knowledge of the competition and co-existence among species (Steinberg and Kareiva, 1997). It has also shown that the distributions of most organisms are not homogeneous throughout their range, but rather occur as patches. Analyses of predator-prey interactions and food-web dynamics are enhanced by considering the habitat association of species. A first step towards this goal is to describe the spatial distributions of the major players in an ecosystem.

The purpose of our study was to examine changes in walleye pollock (*Theragra chalcogramma* (Pallas, 1814)) distribution. Walleye pollock (hereafter called "pollock") are a dominant species in the Gulf of Alaska (GOA). Pollock are the major prey of many species of flatfish and marine mammals and have been the predominant species in Steller sea lion (*Eumetopias jubatus* (Schreber, 1776)) diets since at least the mid-1970s (Pitcher, 1981; Merrick and Calkins, 1996). Numbers of Steller sea lions have declined significantly in recent decades in the western and central GOA. Examination of temporal and spatial changes in the abundance and population structure of pollock is important to understanding the decline in sea lion numbers. Existing and proposed management decisions to protect Steller sea lions include temporal and spatial changes to pollock fishing quotas.

The GOA pollock population peaked in the early 1980s as a result of several strong year classes in the late 1970s (Fig. 1A). Since then, the population has had fewer strong year classes. Modeled estimates of total biomass of the population declined in the early 1980s and leveled off in the 1990s (Fig. 1B). Bottom trawl survey biomass estimates (since 1984) have not reflected the decline in the early 1980s (Fig. 1C). Instead, they showed that the demersal fraction of the population changed little. Compared with other gadoid stocks worldwide, the GOA pollock stock has been lightly exploited; average landings have constituted less than 10% of the stock biomass during the last 20 years (Shima et al., 2000).

In this study we document changes in the spatial distribution and population density of juvenile and adult pol-

lock in the western and central GOA (defined as the area between 147°W and 170°W), from 1984 to 1996. Catch per unit of effort (CPUE) (number of fish/km^2) was used as a measure of density throughout our analysis.

We also examine changes in species associations and the distribution of pollock. Analysis is limited to the summer months because the source of our pollock data were summer research surveys.

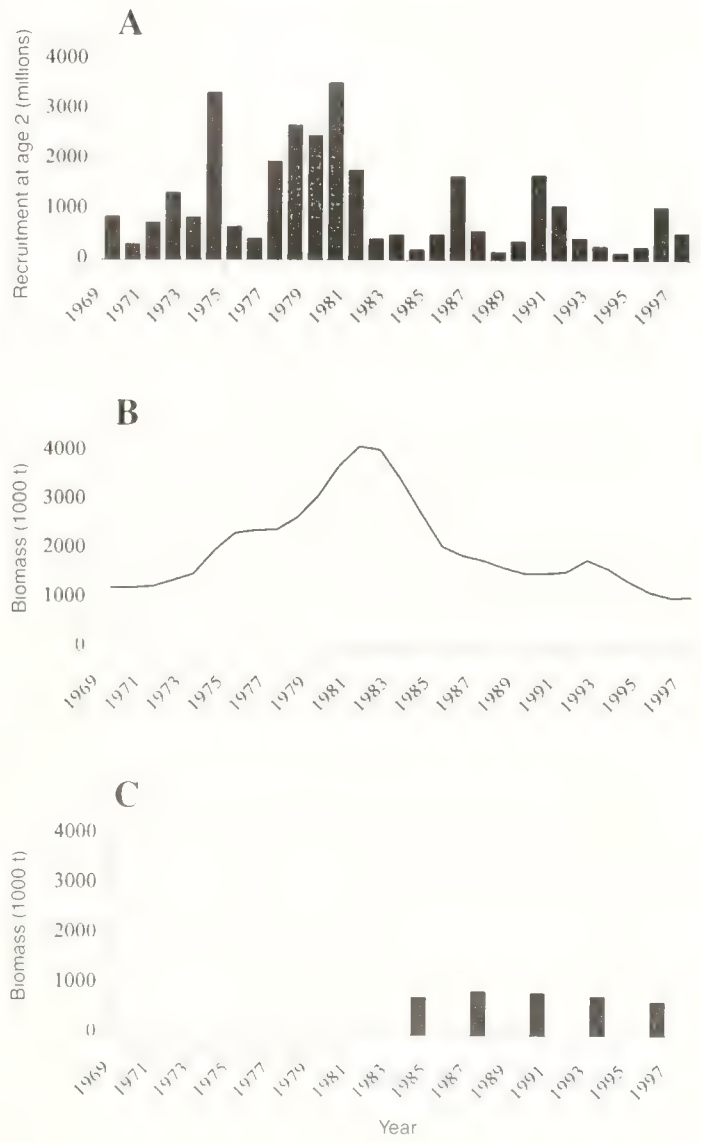

Figure 1

Data for walleye pollock in Gulf of Alaska, 1969–1997: pollock recruitment (**A**), biomass estimates from stock assessment analysis (**B**), and biomass estimates from triennial bottom trawl surveys (**C**). Data are from Dorn, M. W., A. B. Hollowed, E. Brown, B. Megrey, C. Wilson, and J. Blackburn. 2000. Walleye pollock. *In* Stock assessment and fishery evaluation report for the 2000 Gulf of Alaska groundfish fishery, 60 p. North Pacific Fishery Management Council, P.O. Box 103136, Anchorage, Alaska 99510.

Methods

Data source

Data were collected from triennial bottom trawl surveys in the GOA conducted by the Alaska Fisheries Science Center of the U.S. National Marine Fisheries Service (RACE division trawl survey relational database, Mundell[1]). The use of bottom trawl data to assess juvenile pollock abundance and distribution has many precedents. In the Bering Sea, bottom trawl survey data have been used to determine estimates of age-1 pollock, which were used as indices of recruitment (Wespestad[2]). Others have used the same data to evaluate the relationship between juvenile pollock and the movement of the ice edge in the Bering Sea (Wyllie-Echeverria and Wooster, 1998). Bottom trawl estimates have also been used to explore the relationships between different age groups of pollock in Shelikof Strait (Schumacher and Kendall, 1991).

Brodeur and Wilson (1996) modeled the depth distribution of pollock in the GOA during their first year and showed that age-1 pollock were found near bottom. Acoustic surveys of spawning pollock in Shelikof Strait have detected age-1 pollock in both nearbottom and pelagic layers. These data suggest that some age-1 pollock may reside off bottom. Therefore, juvenile pollock data from bottom trawl surveys are used as an index rather than an absolute measure of abundance (Bailey and Spring, 1992; Guttormsen and Wilson[3]).

Survey design

Triennial bottom trawl surveys were conducted during the summer months (May–Sep) of 1984, 1987, 1990, 1993, and 1996. These surveys have consistently been conducted in a stratified random sampling pattern (Martin and Clausen, 1995; Munro and Hoff, 1995; Stark and Clausen, 1995; Martin, 1997). The GOA is divided into 49 strata according to water depth

[1] Mundell, G. 1999. Personal commun. Alaska Fisheries Science Center, NMFS/NOAA, 7600 Sand Point Way NE, Seattle, WA 98115.

[2] Wespestad, V. 1995. Walleye pollock. *In* Plan team for groundfish fisheries of the Bering Sea/Aleutian Islands stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea/Aleutian Islands region as projected for 1996, 35 p. North Pacific Fishery Management Council, P.O. Box 103136, Anchorage, AK 99510.

[3] Guttormsen, M. A., and C. D. Wilson. 1999. Echo integration-trawl survey results for walleye pollock in the Gulf of Alaska during 1998. *In* Stock assessment and fishery evaluation report for the 1998 Gulf of Alaska groundfish fishery, 25 p. North Pacific Fishery Management Council, 605 W 4th Avenue, Suite 306, Anchorage, Alaska 99501.

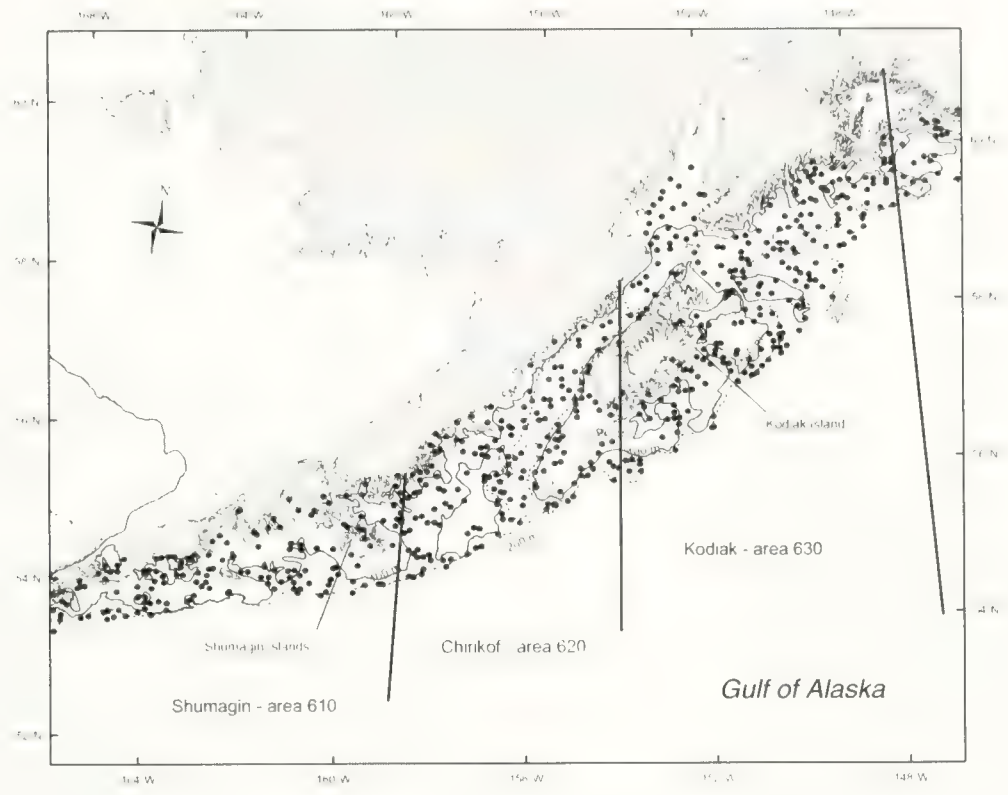

Figure 2

Example of the spatial coverage of the triennial bottom trawl survey for a sample year. Dots indicate station locations.

and area boundaries defined by the North Pacific Fisheries Management Council (http://www.fakr.noaa.gov/rr/figures/fig3.pdf). Allocation of sampling effort within each stratum was based on coefficients of variation, mean CPUE, and sampling densities for all fish species from data collected on previous triennial surveys (see Cochran, 1977). Sampling density within a stratum depended on the anticipated fish density of that particular stratum (Martin and Clausen, 1995; Stark and Clausen, 1995; Martin, 1997). Stations were prioritized within each stratum so that in the event of complications, sampling density would remain controlled. The total survey area was reduced by 7% after 1987 when stations deeper than 500 m were eliminated (Stark and Clausen, 1995). In the interest of consistency, only data from stations less than 500 m in bottom depth were used in our analyses. Station density was spread over a wide range; thus the survey data were most suitable for analyses of geographic distribution and community composition on a large scale (Fig. 2).

For each survey a Nor'eastern trawl (NT) with a 1.25 inch codend liner was used. The liner helped retain juvenile pollock (Brown, 1986). The nylon and polyethylene NTs had net dimensions of 18.3 m wide by 4.7 m high and 18.3 m by 5.5 m, respectively. In 1984 and 1987 a Japanese bottom trawl (JBT) was also used. The horizontal opening of the JBT ranged from 19 to 30 m, the vertical opening from 3.2 to 3.3 m (Brown, 1986). CPUE from the JBT were corrected (using Tables 28 and 31 in Munro and Hoff, 1995) to account for differences between the catchability of the NTs and the JBT.

Data analyses and statistical considerations

Analyses were conducted on total pollock catch as well as on four size groups of pollock: <150 mm (age-0 or young-of-the-year); 150–230 mm (age-1 juveniles); 230–330 mm (age-2 juveniles); and >330 mm (adults). The length-at-age categories were based on a histogram of pollock lengths from a historical database of all NMFS research surveys conducted during the summer. The catchability of age-0 pollock may not have been as high as that for the other juvenile age classes and thus supports the interpretation of all juvenile data as index values (Bailey and Spring, 1992; Guttormsen and Wilson, 1999). Comparable numbers of length measurements were taken every triennial year but measurements were not taken at every station. Thus, analyses of different age groups were based on subsets of the data. The abundance of fish in a specified age category was influenced by year-class strength (Table 1; Megrey et al., 1996; Hollowed et al.[4]). Strong year classes were present in 1984 (age 0), 1990 (age 2), and 1996 (age 2).

[4] Hollowed, A. B., E. Brown, B. Megrey, and C. Wilson. 1996. Walleye pollock. *In* Stock assessment and fishery evaluation report for the 1997 Gulf of Alaska groundfish fishery, 64 p. North Pacific Fishery Management Council, 605 W 4th Avenue, Suite 306, Anchorage, AK 99501.

Table 1

Summary of year-class strength of juvenile walleye pollock in bottom trawl survey years.

	1984	1987	1990	1993	1996
Age 0	Strong	Weak	Weak	Weak	Weak
Age 1	Weak	Weak	Average	Weak	Weak/Average
Age 2	Weak	Strong/Average	Strong	Weak	Strong

Marine surveys typically yield data sets that are highly variable and contain a substantial proportion of zero catches, particularly when the data set is broken down into age groups (Stefansson, 1996). Thus, in some cases the data were analyzed in terms of presence and absence of pollock (hereafter termed "occurrence"). Because nonzero data often follow a lognormal distribution (Pennington, 1996), the lognormal transformations (log(CPUE+1)) of nonzero density data were used during our analyses.

Changes in the depth distribution of pollock were analyzed by 100-m bottom depth intervals, corresponding to the depth stratification used in the triennial surveys. Changes in geographic distribution of CPUE were evaluated by GOA area boundaries, which again corresponded to the stratification design used during the triennial surveys. In our study, three areas were taken into consideration: "Shumagin" (159°–170°W, area 610), "Chirikof" (154°–159°W, area 620), and "Kodiak" (147°–154° W, area 630).

The distribution of pollock in relation to distance from land was evaluated in 20 nautical mile (nmi) increments by using GIS software (ESRI, Inc., 1996). However, the 20-nmi increments crossed the triennial survey strata boundaries, which may have resulted in the disruption of the stratified random sampling scheme. By addressing pollock occurrence or density at each station, instead of biomass, we avoided the need for stratifying the data after collection. Pollock usually reside at depths less than 300 m within the shelf and slope regions of the GOA (NPFMC[5]). Thus, the relatively narrow shelf region would limit the offshore distribution of pollock.

Initial exploratory analyses involved three-dimensional contingency tables to assess the relationship between the occurrence of pollock and year, bottom depth, geographic region, and distance from land. In cases where the three-dimensional analyses rejected the null hypothesis of independence, more detailed partial contingency tables were constructed for the occurrence of pollock against each individual variable. Other studies suggested that bottom depth and geographic location explain most of the variability in fish distribution data (e.g. Overholtz and Tyler, 1985; Jay, 1996).

Single-factor ANOVAs were performed on the nonzero CPUE data to examine the sources of variation in the data. The ln(CPUE+1) of the nonzero data was used as the dependent variable among years. A separate ANOVA was calculated for each category of bottom depth, geographic region, and distance from land.

Examination of the population density data revealed that for most age groups, the number of stations with a low density (<1000 fish/km^2) of pollock increased whereas the number of high-density stations remained relatively stable. This finding suggested that the distribution of suitable habitat for the demersal fraction of the population might have been expanding. Therefore, we examined the distribution of low-density concentrations of pollock separately in relation to the three physical characteristics across the survey years. Although ocean bottom temperature (OBT) was not measured at every survey station, available data were used to help interpret our results. Mean bottom temperature was averaged over bottom depth intervals for each year to provide a general overview (Fig. 3). Additional information on OBT has been summarized by S. Hare (http://www.iphc.washington.edu/staff/hare/html/papers/OBT/obt.html) from a variety of data sources and averaged over five-year periods.

Interspecies associations were examined with Bray-Curtis clustering techniques (Boesch, 1977; Walters and McPhail, 1982). Such classification techniques are useful in generating hypotheses about community structure, which may then be used to aid management actions (Cormack, 1971). Because the surveys used in the cluster analyses were conducted during the summer months, the results could not be extrapolated to other seasons. Triennial survey data were log-transformed and clustered by using the group average fusion strategy. For the species clusters, the top thirty species by weight were chosen in addition to the four age groups of pollock. After careful evaluation of all the cluster dendrograms, a common dissimilarity level (dissimilarity coefficient (h)=27) was chosen for all years as the level at which the most clearly defined clusters occurred throughout the triennial survey years.

Diversity indices were calculated for all five survey years. The top ten species by number of fish were combined for all years to make one list of species for which diversity was analyzed. Simpson's diversity index was calculated both in terms of richness and evenness (Simpson, 1949; Tokeshi, 1993). Richness was interpreted to mean "effective number of species," whereas evenness was un-

[5] NPFMC (North Pacific Fishery Management Council). 1998. Essential fish habitat assessment report for the groundfish resources of the Gulf of Alaska region. NPFMC, 605 West 4th Avenue, Suite 306, Anchorage, AK 99501, 117 p.

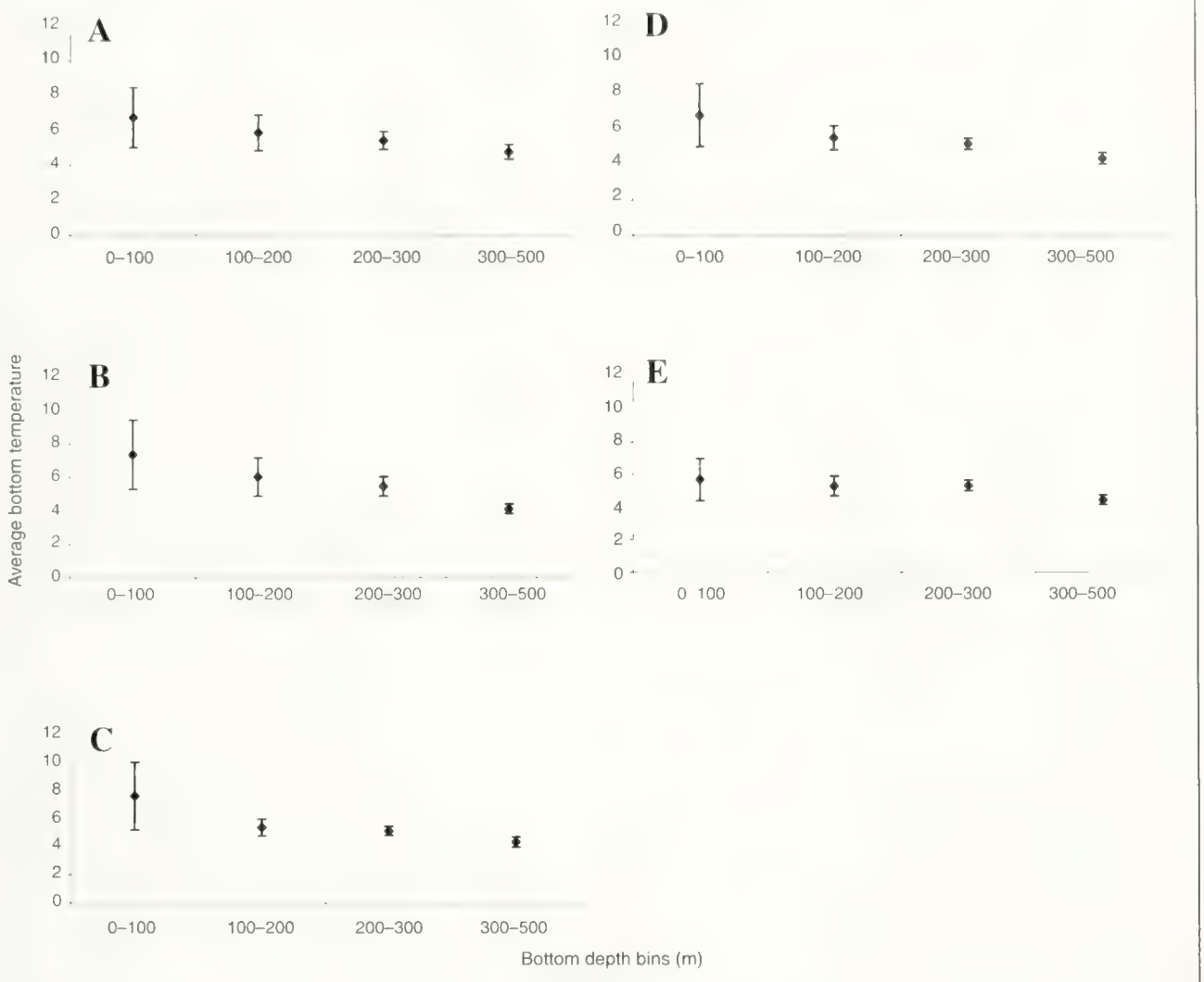

Figure 3

Average bottom temperature by bottom depth category from data collected during the triennial survey; (**A**) 1984, (**B**) 1987, (**C**) 1990, (**D**) 1993, (**E**) 1996. Error bars indicate 1 SD.

derstood to be the "distribution of numbers of fish amongst those species." Confidence intervals were calculated by jack-knifing the diversity index (Magurran, 1988).

Results

All pollock

Three-dimensional contingency tables indicated whether occurrence of pollock was mutually independent of all combinations of bottom depth, geographic region, distance from land, and year. The three-dimensional contingency tables for all three null hypotheses of mutual independence resulted in rejection of the null hypothesis ($P<0.001$). The null hypotheses considered for the three-dimensional and partial contingency tables are listed in Table 2. A summary of the distribution of stations within categories of the three physical characteristics is given in Table 3. All the hypotheses of partial independence on combinations of two of the physical characteristics could be rejected ($P< 0.001$). When each physical characteristic was tested separately, the only hypothesis that could not be rejected ($\alpha=0.05$) was the independence of pollock occurrence against geographic region ($P=0.097$, Table 2). Graphs of pollock occurrence versus each of the physical characteristics revealed distinctive patterns (Fig. 4). The graphs indicated that pollock are most frequently observed in the 100–200 m bottom depth interval and the 0–20 nmi distance category (Fig. 4, A and B). However, this interpretation may be an artifact of the percentage of stations sampled within each category (Table 3). For all years, the

greatest number of stations were sampled in the 100–200 m bottom-depth category and in the 0–20 nmi distance–from-land category.

The results were standardized by taking the proportion of stations within each category that had a positive occurrence of pollock (Fig. 5). These graphs showed that for each bottom depth category, the proportion of positive occurrences had increased over the years. The proportion of stations where pollock were present was consistently high in the 0–20 nmi category (Fig. 5). Farther from land, the proportion of positive stations increased between 1984 and 1996. In all three geographic regions, there was an increase in the proportion of stations where pollock were present.

Table 4 lists the number of hauls with pollock occurrence and summarizes the CPUE values for the nonzero data. Results from the single-factor ANOVAs calculated for the nonzero density data are summarized in Table 5. Significant differences were observed among most years, except for the Chirikof region and the distances from land of 0–20 and 40–60 nmi.

Table 2

Contingency table analysis of walleye pollock occurrence.

Type of table	*P*-value
Three-dimensional tables of mutual independence	
Null hypothesis	
Pollock occurrence, year, and bottom depth are mutually independent	$P< 0.001$
Pollock occurrence, year, and distance from land are mutually independent	$P< 0.001$
Pollock occurrence, bottom depth, and region are mutually independent	$P< 0.001$
Pollock occurrence, region, and distance from land are mutually independent	$P< 0.001$
Three-dimensional tables of partial independence	
Null hypothesis	
Pollock occurrence is independent of year and bottom depth	$P< 0.001$
Pollock occurrence is independent of year and distance from land	$P< 0.001$
Pollock occurrence is independent of bottom depth and region	$P< 0.001$
Pollock occurrence is independent of region and distance from land	$P< 0.001$
Two-dimensional tables of partial independence	
Null hypothesis	
Pollock occurrence is independent of year	$P< 0.001$
Pollock occurrence is independent of bottom depth	$P< 0.001$
Pollock occurrence is independent of region	$P=0.097$
Pollock occurrence is independent of distance from land	$P< 0.001$

Adult pollock

The initial three-dimensional contingency tables of mutual independence between adult pollock occurrence and the three physical characteristics proved significant. Subsequent contingency analyses revealed significant results for all partial independence tests except for the two-dimensional test for independence between occurrence of adult pollock and geographic region (P=0.58).

Examination of all the positive data showed that the mean of the log-transformed CPUE decreased and the variance increased over time for bottom depths 100–200 m in each geographic area (Table 6). The mean CPUE also decreased over time for stations <40 nmi from land but there was no trend in the changes in variance (Table 6). The ANOVA confirmed that changes in the distribution of pollock from 1984 to 1996 were significant (α=0.05) among years at all depth intervals, all geographic areas , and at a distance from land <60 nmi (Table 7). Thus, although the number of stations where pollock could be encountered increased (e.g. the low-density distribution data), the mean adult pollock density decreased and became more variable between 1984 and 1996 (Fig. 5, Table 6).

Changes in the distribution of adult pollock were further examined by sorting the data into seven CPUE bins and by making histograms of the frequency of stations within each bin (Fig. 6). The histogram revealed that over the years, the occurrence of stations with zero adult pollock CPUE decreased, whereas stations with low-density (CPUE <1000 fish/km^2) concentrations of pollock increased. Higher density stations did not exhibit any particular trend.

To better understand observed changes in the distribution of low-density concentrations of adult pollock, all the stations were characterized by bottom depth, geographic location, and distance from land (Fig. 7). The number of stations that had low-density concentrations of adult pollock increased in all habitat categories over the years. The proportion of stations within each bottom depth bin with low-density concentrations of adult pollock more than doubled from 1990 to 1996. Comparable dramatic increases were observed with regard to distance from land and geographic region.

Juvenile pollock

Contingency table analysis for juvenile pollock occurrence resulted in significant (P<0.001) results across all ages for tests of mutual independence among all the physical characteristics. Two-dimensional contingency analyses also resulted in significant results. It was difficult to discern any chronological trends in the mean and variance of all the positive data for juvenile pollock. Minor fluctuations in juvenile pollock density may have been related to interannual differences in year-class strength (Table 1).

Histograms similar to those for adult pollock were made for all three juvenile age groups of pollock, where juvenile

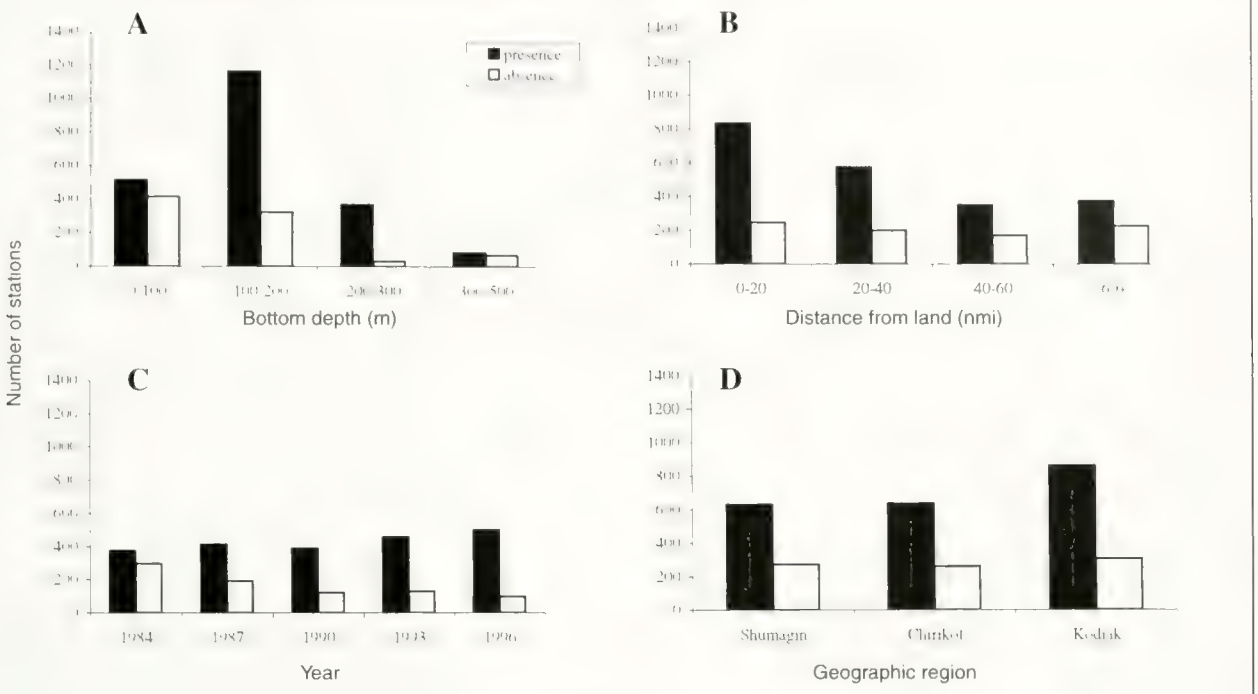

Figure 4

The number of stations at which walleye pollock occurred by physical characteristic: (**A**) bottom depth (m); (**B**) distance from land (nmi); (**C**) year; and (**D**) geographic region.

Table 3

Summary of the percentage of stations within each bin for the three types of physical parameters discussed in the text. The number in parentheses indicates the total number of stations.

	Percentage of stations in category by year				
Physical category	1984 (749)	1987 (648)	1990 (534)	1993 (616)	1996 (613)
Bottom depth (m)					
0–100	29.9	33.7	23.7	32.8	35.4
100–200	46.1	53.7	59.1	50.9	43.2
200–300	16.5	9.6	13.8	12.0	14.7
300–500	7.4	3.0	3.4	4.3	6.7
Geographic location					
Shumagin	33.2	28.5	26.7	29.3	33.7
Chirikof	27.5	32.5	30.8	29.5	30.9
Kodiak	39.3	40.0	42.5	41.2	35.4
Distance from land category (nmi)					
0–20	28.9	39.3	36.2	38.1	40.6
20–40	27.2	25.7	25.5	27.4	23.9
40–60	19.2	16.9	20.4	16.6	14.3
60+	24.7	18.1	17.9	17.8	21.1

pollock density was parsed into bins and plotted (Fig. 8). The same trend seen in the adults was also seen with the juvenile pollock. As the years progressed, there was an increase in the proportion of stations that had low-density (<1000 fish/km^2) concentrations of all juvenile age groups of pollock. For age-0 and age-1 pollock, there was about a tenfold difference in the proportion of stations with low-density concentrations after 1987 (Fig. 8). Age-2 pollock

Table 4

Summary information of walleye pollock occurrence and CPUE by triennial survey year. CPUE values are given in number of fish/km^2 and summarize only the nonzero positive tows.

	Number of hauls		CPUE			
Year	Total	Pollock present	Minimum	Maximum	Mean	SD
1984	672	375	11.48	397079.10	9759.45	31564.10
1987	603	412	13.85	602901.72	9640.16	43282.89
1990	506	386	16.77	130009.85	6866.74	15946.86
1993	583	454	19.03	218130.41	4994.91	15947.79
1996	593	497	32.22	239402.07	5434.23	18829.21

Table 5

Single-factor ANOVAs of ln(CPUE+1) of positive walleye pollock catches among years by bottom depth category, geographic region, and distance from land. SS = sum of squares; MS = mean square.

	SS	df	MS	*F*	*P*
Bottom depth (m)					
0–100	73.60	4	18.40	3.37	0.01
100–200	91.04	4	22.76	4.24	<0.001
200–300	77.22	4	19.31	6.47	<0.001
300–500	19.00	4	4.75	3.19	0.02
Geographic area					
Shumagin	84.68	4	21.17	3.94	<0.001
Chirikof	24.29	4	6.07	1.16	0.33
Kodiak	185.06	4	46.27	10.47	<0.001
Distance offshore (nmi)					
0–20	23.80	4	5.95	1.21	0.30
20–40	71.94	4	17.99	3.51	0.01
40–60	29.94	4	7.49	1.66	0.16
60+	56.66	4	14.17	3.99	<0.001

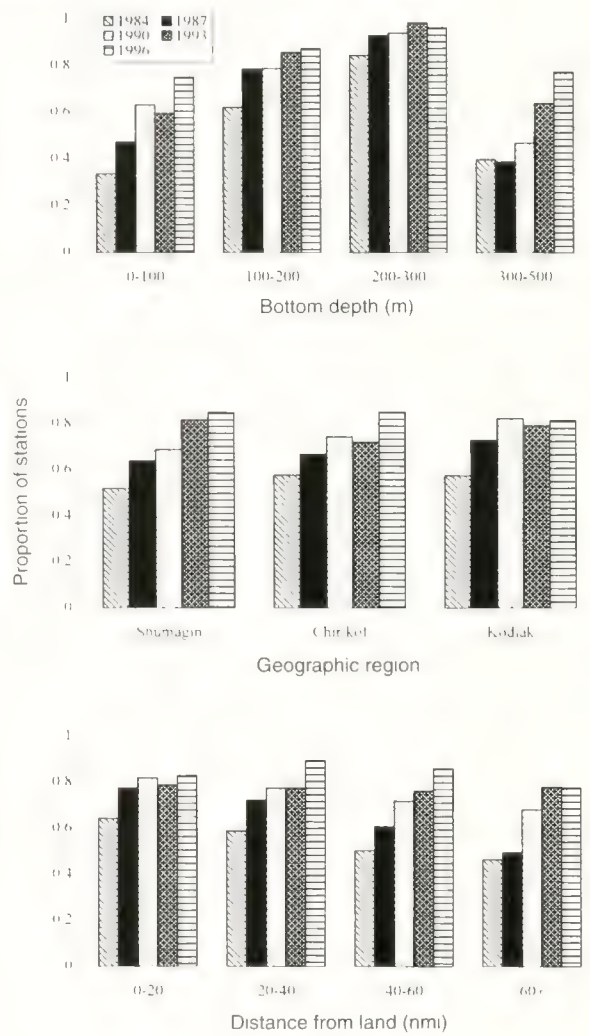

Figure 5

The proportion of stations within each category of physical characteristic where walleye pollock were found .

also exhibited this trend but not to the same degree as age-0 and age-1 pollock.

Stations with low-density concentrations of juvenile pollock were examined with respect to bottom depth, geographic area, and distance from land (Fig. 9). For all ages of juvenile pollock there was a marked difference between 1984–87 and the 1990s. A greater proportion of stations with age-0 pollock was observed at bottom depths <200 m than at deeper depths, especially in 1996. Age-0 pollock occurrence increased in the Chirikof and Shumagin regions before also increasing in the Kodiak region in 1996. Age-0 pollock also occurred more frequently at distances <60 nmi from land.

In 1990, the proportion of stations with low-density concentrations of age-1 pollock increased the most at bottom depths >200 m, before the same increasing trend was also observed at shallower bottom depths in 1993 and 1996 (Fig. 9). The increase was observed across all geographic regions and at all distances from land.

Table 6

Mean and variance estimates of ln(CPUE+1) for 1984–96 for nonzero adult pollock data by physical characteristic. The number of observations is given in parentheses.

	Mean					Variance				
Physical characteristic	1984	1987	1990	1993	1996	1984	1987	1990	1993	1996
Bottom depth (m)										
0–100	8.05 (24)	8.59 (37)	7.05 (23)	6.73 (74)	6.41 (108)	3.45	2.80	3.87	7.71	5.38
100–200	8.84 (121)	8.66 (110)	8.17 (158)	6.74 (204)	6.20 (192)	2.77	2.43	2.56	3.81	4.23
200–300	7.82 (52)	8.14 (24)	7.68 (60)	6.58 (64)	5.88 (82)	2.40	0.70	1.59	1.68	1.69
300–500	7.02 (1)	0 (1)	7.43 (1)	5.28 (12)	4.70 (30)	0	0	0	0.30	0.88
Geographic area										
Shumagin	8.80 (63)	8.45 (37)	7.40 (33)	6.63 (101)	6.32 (121)	2.65	2.35	2.30	5.54	3.72
Chirikof	8.09 (57)	8.62 (49)	7.91 (52)	6.65 (83)	5.74 (125)	3.64	2.47	2.65	3.23	3.71
Kodiak	8.47 (78)	8.62 (82)	8.22 (134)	6.91 (138)	6.42 (138)	2.53	2.23	2.50	3.94	4.21
Distance from land (nmi)										
0–20	8.49 (141)	8.67 (140)	8.04 (161)	7.02 (236)	6.40 (269)	2.90	2.15	2.76	4.42	4.28
20–40	8.50 (42)	7.76 (19)	7.59 (57)	5.79 (96)	6.12 (86)	3.57	2.33	1.93	2.75	1.36
40–60	8.16 (13)	8.66 (10)	5.31 (16)	6.23 (20)	8.00 (40)	1.88	3.46	2.20	2.52	2.24
60+	5.38 (2)	5.95 (2)	8.26 (8)	6.66 (10)	5.66 (7)	4.54	4.55	2.53	4.42	2.55

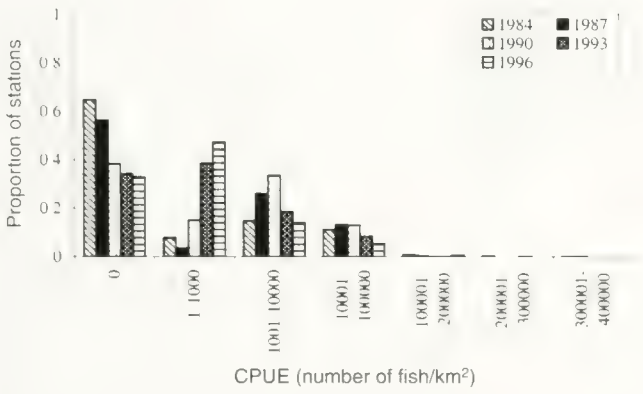

Figure 6

Porportion of stations for different density levels of adult walleye pollock.

Table 7

Single-factor ANOVAs of ln(CPUE+1) of positive adult walleye pollock catches among years by bottom depth category, geographic region, and distance from land. SS = sum of squares; MS = mean square.

	SS	df	MS	*F*	*P*
Bottom depth (m)					
0–100	162.23	4	40.56	7.55	<0.001
100–200	872.70	4	218.17	65.99	<0.001
200–300	196.38	4	49.09	30.76	<0.001
300–500	37.80	4	9.45	13.04	<0.001
Geographic area					
Shumagin	345.66	4	86.42	22.87	<0.001
Chirikof	448.03	4	112.01	34.19	<0.001
Kodiak	453.24	4	113.31	35.09	<0.001
Distance (nmi)					
0–20	758.52	4	189.63	53.61	<0.001
20–40	417.66	4	104.41	40.42	<0.001
40–60	174.97	4	43.74	18.59	<0.001
60+	30.82	4	7.70	2.48	0.071

There was a general increase over time of low-density concentrations of age-2 pollock with respect to bottom depth and geographic region (Fig. 9). The increase in the proportion of low-density concentrations of age-2 pollock was the greatest 20–60 nmi from land until 1996, when the proportion of stations with low-density concentrations increased the most >60 nmi from land.

Community composition

Results of clustering by species by using the triennial bottom trawl data are presented in Table 8. The top 30 species or species types (e.g. adult and juvenile pollock) by weight over all survey years were chosen. Adult pollock were consistently associated over the years most closely with flathead sole (Table 8). The cluster containing adult pollock usually included 3–6 other species of importance, either commercially or in terms of abundance. These included arrowtooth flounder (*Atheresthes stomias* (Jordan

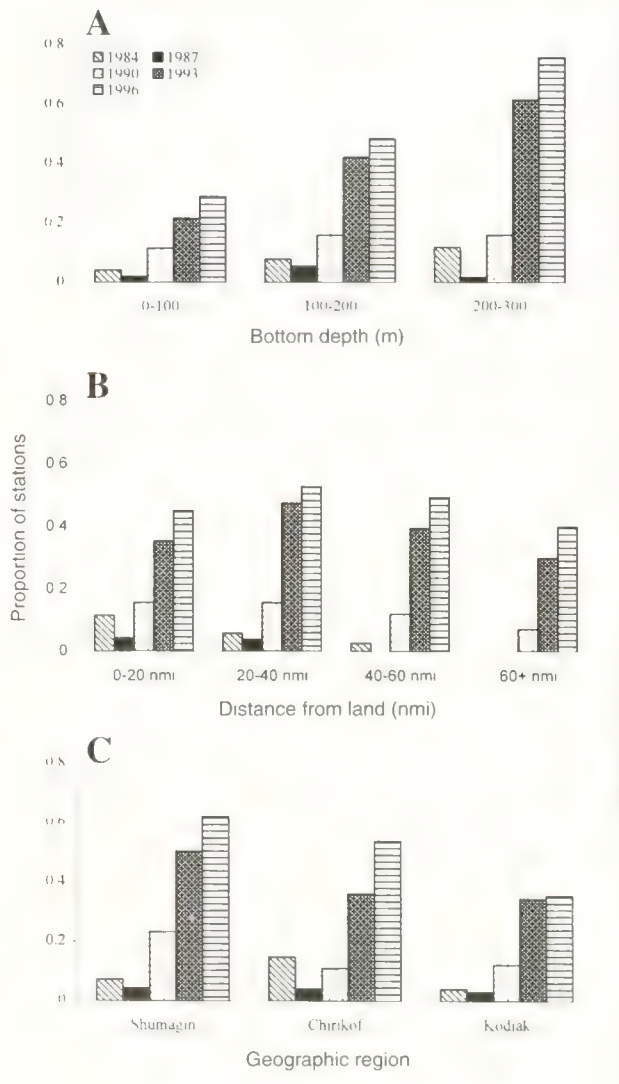

Figure 7

Proportion of stations where low-density concentrations (<1000 fish/km^2) of adult walleye pollock were observed, binned by bottom depth (**A**), distance from land (**B**), and geographic region (**C**).

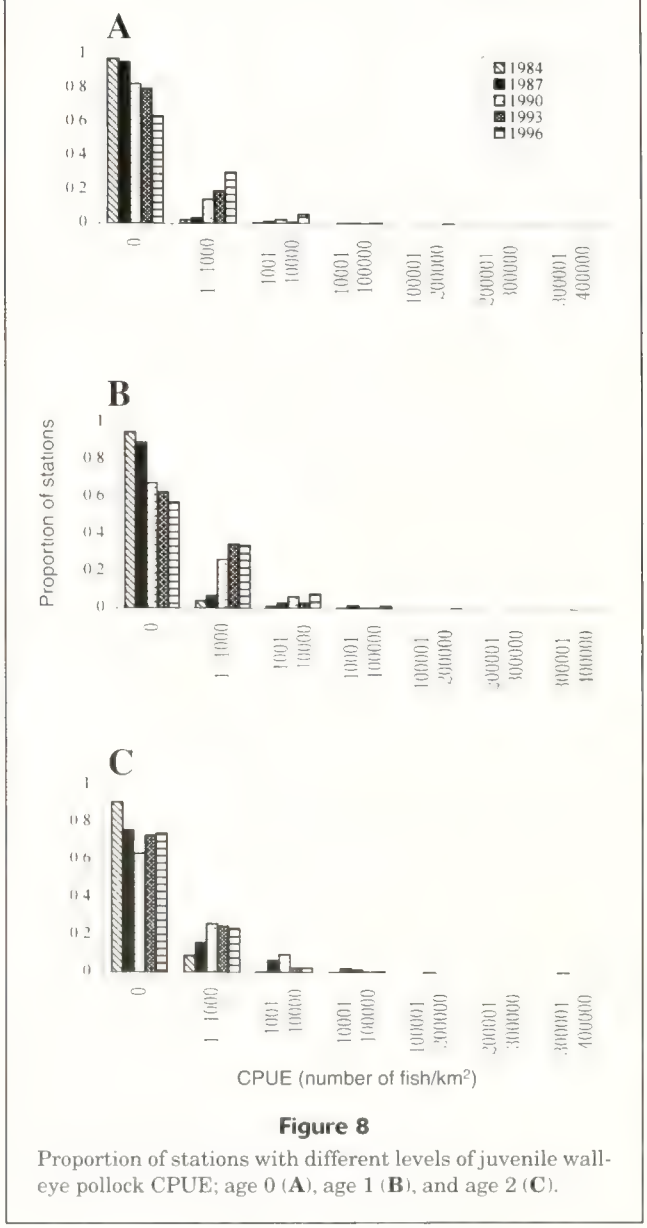

Figure 8

Proportion of stations with different levels of juvenile walleye pollock CPUE; age 0 (**A**), age 1 (**B**), and age 2 (**C**).

and Gilbert, 1880)), Pacific halibut (*Hippoglossus stenolepis* Schmidt, 1904), Pacific cod (*Gadus macrocephalus* Tilesius, 1810), sablefish (*Anoplopoma fimbria* (Pallas, 1814)), Dover sole (*Microstomus pacificus* (Lockington, 1879)), and rex sole (*Glyptocephalus zachirus* Lockington, 1879). This small cluster was usually isolated from the larger main cluster (i.e. high dissimilarity between the two clusters). Adult pollock were also clustered separately from the juvenile pollock age groups. In all years except 1987, age-1 and age-2 pollock were clustered with each other, whereas age-0 pollock were clustered separately. In 1987, age-0 and age-1 pollock clustered together, although not as closely associated as ages 1 and 2 in the other years. Until 1996, age-0 pollock clustered with Pacific sleeper shark (*Somniosus pacificus* Bigelow and Schroeder, 1944), Aleutian skate (*Bathyraja aleutica* (Gilbert, 1896)), or silvergray rockfish (*Sebastes brevispinis* (Bean, 1884)). In the larger cluster that contained all the juvenile pollock age groups, it was common to find Pacific herring (*Clupea pallasii* (Cuvier and Valenciennes, 1847)) in all years.

Cluster analysis by station of the triennial data resulted in clusters that fell into clean zoogeographic groups that followed depth contours. Maps of clusters identified seven groups of species that could be tracked in the GOA throughout most years (Table 9). Groups 1, 2, and 5 were present only in 4 out of the 5 triennial survey years. In 1984, groups 2 and 5 were absent whereas in 1990, group 1 was absent. The species within each cluster were listed in order of dominance. Although many of the clusters had

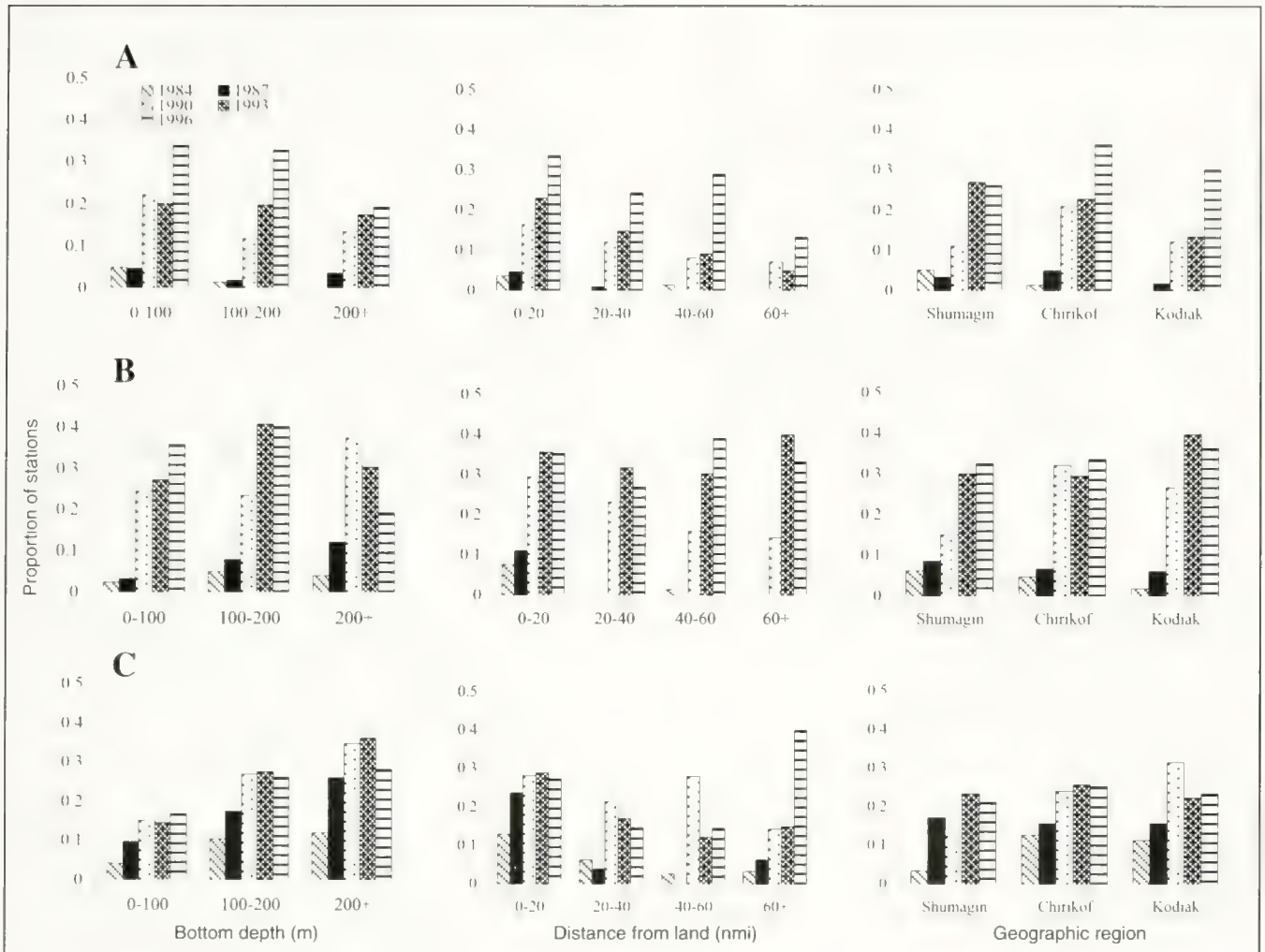

Figure 9

Proportion of stations with low-density concentrations (<1000 fish/km^2) of juvenile pollock by bottom depth (first column), distance from land (second column), and geographic region (third column) for age 0 (**A**), age 1 (**B**), and age 2 (**C**) juveniles.

the same main species in common, as listed in Table 9, differences in dominance distinguished the various clusters. Adult pollock were most dominant in groups 1, 3, and 6, which were either made up of nearshore or deep shelf stations (Table 9). Mean values of several environmental variables in these station groups in which pollock were found indicate that bottom depth and temperature varied (Table 9). Shallow water stations (groups 1 and 2) were grouped into warm (6.4°C) and average (5.7°C) bottom temperature clusters (Table 9). As expected, deeper water stations tended to be characterized by cooler temperatures. Juvenile (ages 0–2) pollock were found mostly in the nearshore stations.

Diversity

Separate diversity indices were calculated for habitat between 0–100 m bottom depth and 100–200 m bottom depth. In the 0–100 m habitat, there was a slight decrease in richness from 9–10 in the 1980s to 7–9 effective number of species in the 1990s (Fig. 10A). Calculations of evenness for the same data indicated that there had been little change in the evenness component of species diversity in the 0–100 m habitat (Fig. 10C). Histograms of the proportion (in terms of number of fish) contributed by each of the top species indicated that the decrease in richness might partially be explained by an increase in the predominance of pollock and a decrease in the presence of rockfish species (Fig. 11, A–E).

Richness in the 100–200 m category increased from 5 to 10 effective numbers of species (Fig. 10B). The predominance of pollock and arrowtooth flounder in the 1980s had shifted to include eulachon (*Thaleichthys pacificus* (Girard, 1858)) and Pacific ocean perch (*Sebastes alutus* (Gilbert, 1890); Fig. 11, F–J). Evenness was relatively consistent throughout the survey years (Fig. 10D).

Discussion

A major result of our study was that for all age groups of pollock, the number of stations where pollock occurred at low densities (<1000 fish/km^2) increased during 1984–96 while the mean density decreased. This pattern suggests that the pollock population was increasing its range, a characteristic often seen in growing populations that is consistent with the "basin hypothesis" (MacCall, 1990). MacCall hypothesized that at low-densities, marine fish will occupy habitats that are optimal for survival. As populations grow, however, some portions of the populations will expand into locations of less suitable habitat quality.

Our analyses of the data indicated that the demersal portion of the pollock population was stable but that the overall (pelagic and demersal) pollock population declined during the study (1984–96, Fig. 1, B and C). Year-class strength was only sporadically strong and therefore would not account for the sustained increased positive occurrence by station during the early- to mid-1990s. Under MacCall's hypothesis, the range of the population should have been stable or contracting. Thus, patterns emerging from our data are not entirely consistent with MacCall's model.

Analysis of CPUE of all positive tows revealed that there was a decrease in mean CPUE over the years from 1984 to 1996. The data showed an increase in low-density concentrations of adult pollock stations across all categories but in particular at bottom depths 200–300 m and in the Chirikof and Shumagin regions. We conclude that adult pollock had expanded into deeper water in the 1990s but that the expansion had resulted in a decrease of adult pollock in high-density stations, combined with decreased mean density of adult pollock throughout the region. We hypothesize that the expansion of pollock was due to an increase in the suitability of habitats for adult pollock, possibly caused by a spread in the distribution of pollock forage, during a period of stable or decreasing pollock population trends. If predators of pollock rely on high-density patches, the decreased mean density of pollock may have negative ramifications for the successful foraging of top predators. We refer to this as the "forage density hypothesis"; i.e. habitat suitability has changed, perhaps on a local scale, such that there has been an expansion of the overall population distribution. However, the expansion, combined with decreasing population numbers, had caused the density of pollock patches to decrease below a threshold at which top predators can successfully forage. The underlying assumption here is that the predators need patches of high prey density rather than a uniform distribution of average or low prey density.

Analysis of trends in the distribution and abundance of juvenile age groups is more difficult because data for

Table 8

Species associated with walleye pollock according to Bray-Curtis cluster analyses of triennial survey data. The species are listed in order of association.

Adults	Age 0	Ages 1 and 2
Flathead sole	Pacific sleeper shark	Atka mackerel
Sablefish	silvergray rockfish	eulachon
Dover sole	lingcod	Pacific herring
Rex sole	longnose skate	bigmouth sculpin
Arrowtooth flounder	sharpchin rockfish	lingcod
Pacific halibut	Pacific herring	chinook salmon
Pacific cod		

Table 9

Description of consistent station groups found as a result of cluster analyses of the triennial bottom trawl survey data. The group designation "flatfish" includes all flatfish except arrowtooth flounder. Mean values are given for the environmental variables. Standard deviations are given in parentheses.

Group no.	Location	Bottom depth (m)	SST (°C)	Temperature at depth (°C)	Main species
1	Nearshore 1	85.9 (32.1)	9.7 (2.4)	5.7 (4.9)	Age 2 and Adult pollock, Flatfish
2	Nearshore 2	83.7 (38.4)	9.4 (2.4)	6.4 (1.7)	Adult pollock, Flatfish, Pacific cod
3	Shallow shelf	119.9 (47.7)	9.0 (2.5)	5.8 (1.9)	Arrowtooth flounder, Adult pollock, Pacific halibut, Pacific cod
4	Deep shelf	120.6 (31.9)	9.5 (2.2)	5.5 (0.7)	Arrowtooth flounder, Flatfish, Pacific cod, Adult pollock
5	Inner slope	167.0 (50.3)	10.9 (2.2)	5.6 (0.8)	Northern rockfish, Pacific ocean perch, Arrowtooth flounder
6	Middle slope	197.1 (80.4)	10.1 (2.9)	5.3 (0.7)	Adult pollock, Pacific ocean perch, Arrowtooth flounder, Sablefish
7	Outer slope	412.9 (153.5)	10.7 (3.1)	4.9 (0.9)	Giant grenadier, Sablefish, Rockfish

these age groups are strongly influenced by interannual variations in year-class strength. However, spatial trends in distribution were consistent with those seen for adult pollock. For all age groups of juvenile pollock there was an increase in the proportion of stations where low densities occurred, and a decrease in the mean CPUE during the time period examined.

The spatial expansion by a species should be reconciled with more detailed analyses of the characteristics of the area it occupied to determine whether changes in habitat suitability have occurred. Adult pollock are not expanding into areas with physical characteristics previously not associated with pollock. Cluster analysis revealed that adult pollock are associated with average bottom temperatures between 5.2°C and 6.4°C. The bottom temperature data from field surveys revealed a consistent range over time of 5–6°C (Dorn et al.[6]). It was difficult to discern a trend from either our bottom temperature or the OBT data. Temperatures may have been slightly warmer in the 1980s than in the 1990s. Temperature changes, together with the shoaling of the mixed layer depth (Polovina et al., 1995; Shima, 1996), may have caused a redistribution of prey, possibly contributing to changes in pollock distribution.

Evidence of the importance of external forcing on the spatial range of fish species has been noted in other ecosystems. Movement of fish in response to environmental change was recorded in the Barents Sea when Atlantic cod (*Gadus morhua* Linnaeus, 1758) shifted westward as a consequence of cooler waters (entering from the east) across the region from 1977–81 (Loeng, 1989). Primary shifts in distribution, in response to temperature changes, were seen in younger age classes of fish. Because there were some species (e.g. haddock, *Melanogrammus aeglefinus* (Linnaeus, 1758)) that did not respond to changes in temperature, it may be that the movement of the fish may be dependent on the sensitivity of fish prey to the temperature shifts (Shevelev et al., 1987). Cod (like pollock) feed mostly on planktonic organisms that may respond rapidly to temperature changes whereas haddock feed mostly on benthic species (Shevelev et al., 1987).

External forcing may also include anthropogenic factors. Domestication (U.S.) of the pollock fishery occurred during the period investigated (Megrey, 1989) with the result that fishing operations shifted from at-sea processors

[6] Dorn, M. W., A. B. Hollowed, E. Brown, B. Megrey, C. Wilson, and J. Blackburn. 1999. Walleye pollock. *In* Stock assessment and fishery evaluation report for the 2000 Gulf of Alaska groundfish fishery, 65 p. North Pacific Fishery Management Council, P.O. Box 103136, Anchorage, Alaska 99510.

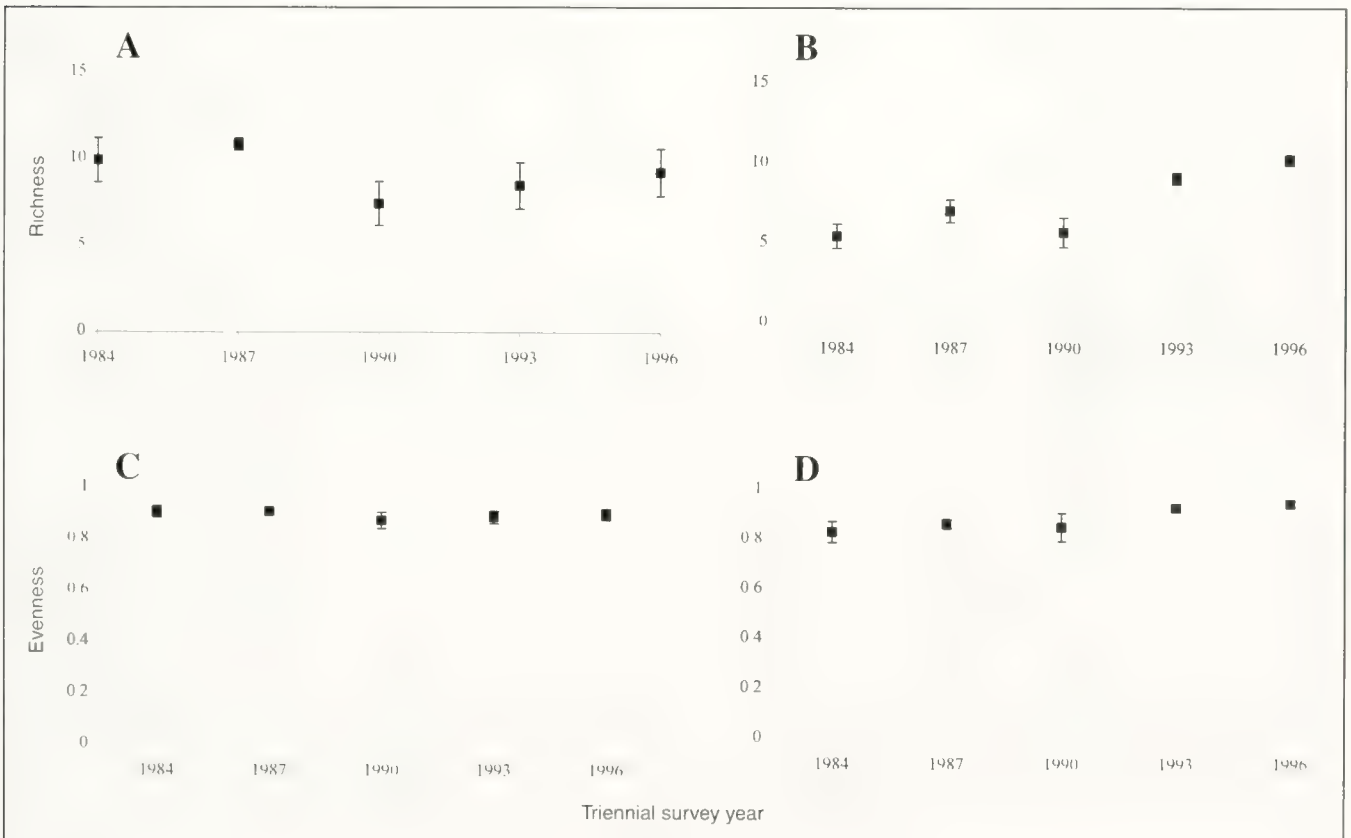

Figure 10

Simpson's diversity indices: richness for the 0–100 m bottom depth (**A**) and for the 100–200 m bottom depth (**B**); evenness for the 0–100 bottom depth (**C**) and for the 100–200 m bottom depth (**D**). Error bars indicate 1SD.

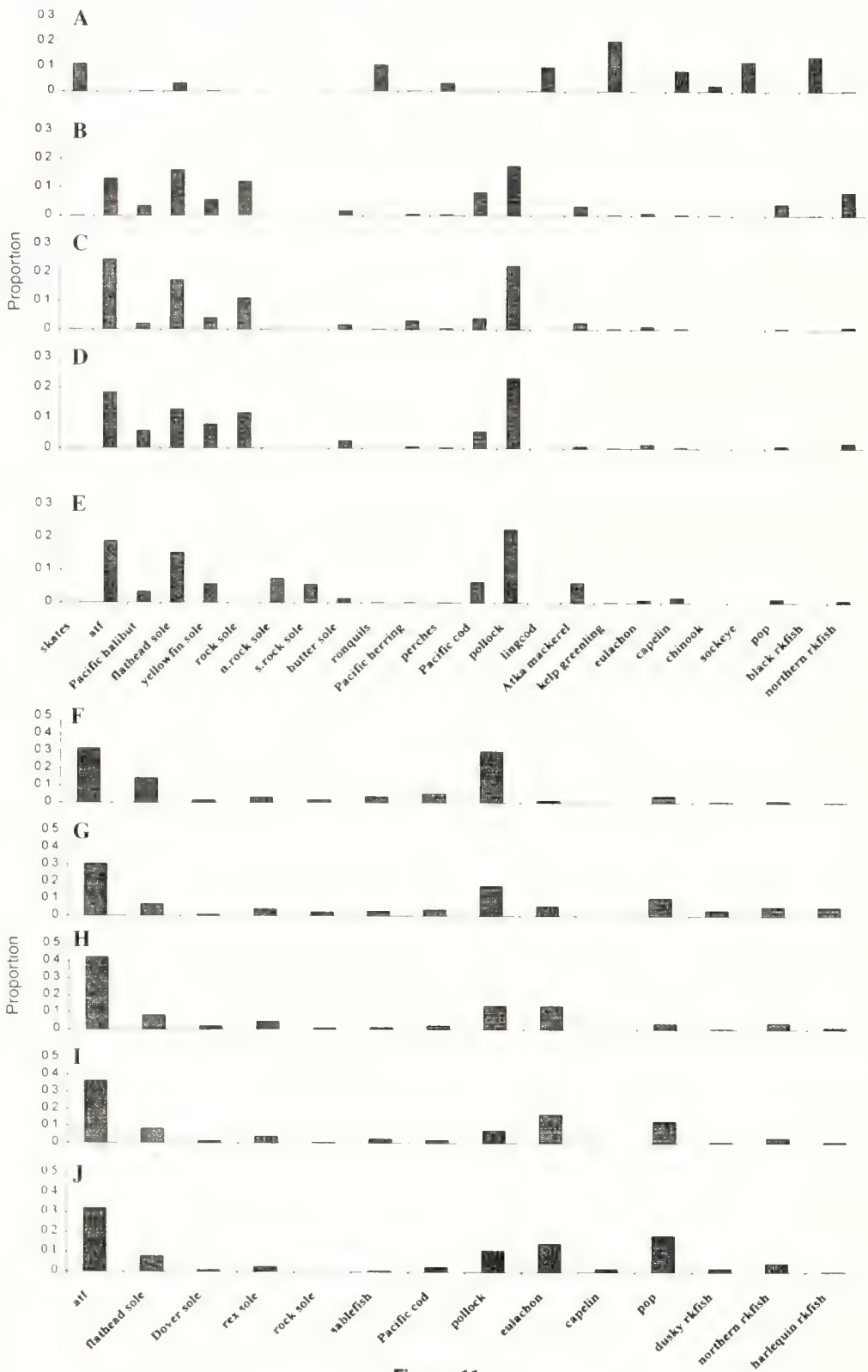

Figure 11

Proportion of the top species included in the diversity index calculations for 1984–96 in the 0–100 m bottom depth interval (**A–E**) and the 100–200 m bottom depth interval (**F–J**). Some fish species names have been abbreviated: atf = arrowtooth flounder, n. rock sole = northern rock sole, s. rock sole = southern rock sole, pop = Pacific ocean perch, rkfish = rockfish.

to a reliance on shoreside processing. The shift moved fishing operations closer to shore after the mid-1980s (Fritz[7]). Studies in other regions have found that groundfish species (Pacific whiting and haddock) disperse as a result of trawling. However, within minutes of a vessel's passage, the fish usually revert back to their original distribution (Ona and Godøø, 1990; Nunnallee[8]). It should be noted that this behavior is the result of disturbance by a single vessel. It is possible that the activity of multiple vessels that make up commercial fisheries could cause long-term redistribution of pollock. Studies are currently underway to examine the potential effect of commercial fisheries on the distribution of pollock (Hollowed et al.[9]).

Predator-prey interactions also influence the distribution of marine fish. Adult pollock are capable of exhibiting a strong top-down influence on juvenile abundance through cannibalism (Livingston, 1991). However, in the GOA the incidence of cannibalism is minimal (Yang, 1993), perhaps because, as shown in our study, the ranges of adult and juvenile pollock do not overlap. Spatial distributions showed that the bulk of both adult and juvenile pollock occurred in the Kodiak and Chirikof regions in the GOA. Mean density for both juveniles and adults was high within 20 nmi from land. However, age-0 (and often age-1) pollock were in greatest density in shallow waters <20 nmi from land, whereas adult pollock tended to occupy deeper waters. Age-2 pollock, which are beyond the size range that adult pollock target as food in the Bering Sea, tend to have a distribution similar to that of adults. The separation between juveniles and adults could be a seasonal effect due to the summer sampling season of the surveys because juvenile pollock are known to migrate ontogenetically (Brodeur and Wilson, 1996). However, the pattern of spatial separation between age-0 and age-1 pollock and adult pollock may indicate avoidance of adults by juvenile pollock.

An examination of changes in density of juvenile pollock in relation to geographic location allowed evaluation of the prevailing conceptual model for pollock ontogeny in the Gulf of Alaska (Kendall et al., 1996). The majority of spawning for the GOA stock occurs in the Shelikof Strait region (Kendall and Picquelle, 1989; Hinckley et al., 1991; Kendall et al., 1996). Survey and ocean modeling studies show that larvae and early juveniles are advected by the Alaska Current towards the Shumagin Islands (Hinckley et al., 1991; Hermann et al., 1996; Hinckley, 1999). Our results are partially consistent with the conceptual model for pollock ontogeny: the area encompassing Shelikof Strait and west to the Shumagin Islands (i.e. the Kodiak and Chirikof regions) was important for all juvenile age groups. However, the disproportionate increase of pollock in the Kodiak region in the 1990s, with two strong year classes (1988 and 1994), supports the suggestion that substantial spawning may also occur outside of Shelikof Strait (Smith et al., 1984; Brodeur and Wilson, 1996).

The species composition of the cluster in which pollock was included changed little over the course of the survey years. Adult pollock were usually located together with commercially important flatfish, arrowtooth flounder, and Pacific cod. This finding is consistent with other findings from the eastern Bering Sea where pollock often were associated with snow and Tanner crabs (*Chionoecetes* spp.), Pacific cod, flathead sole, Greenland turbot (*Reinhardtius hippoglossoides* (Gill, 1861)), and yellowfin sole (*Limanda aspera* (Pallas, 1814)) from 1978 to 1981 (Walters and McPhail, 1982).

Depth contours served as demarcations of station clusters in our study as well as in others conducted in the eastern Bering Sea and the eastern Pacific Ocean along the western coast of the United States (Gabriel and Tyler, 1980; Walters and McPhail, 1982; Jay, 1996). The consistency in how the stations were grouped together is common throughout all these studies. Walleye pollock in the eastern Bering Sea also dominated clusters of stations in the central shelf or the outer shelf. Other species commonly found together with pollock in these groups were yellowfin sole and Pacific cod.

A hypothesis relating pollock distribution to sea lion foraging behavior

Because pollock predominate the Steller sea lion diet (Merrick and Calkins, 1996), the temporal and spatial changes in pollock abundance and distribution could affect Steller sea lions. The Steller sea lion population underwent precipitous declines in the 1980s and declines continued in the 1990s but not as steep (Sease et al., 1999; NMFS[10]). The rate of decline continues to be high towards the center of the Gulf of Alaska (150–158°W), whereas the western Gulf region (158–162°W) has stabilized (i.e. the rate of decline has decreased).

Survey results suggest that the "forage density hypothesis" may apply to Steller sea lions in the GOA. There is evidence indicating that Steller sea lions target dense aggregations of prey (Sinclair and Zeppelin, in press), so that the lower mean density of pollock may reduce the number of successful Steller sea lion foraging trips in the central GOA. This effect may have prevented the sea lion population from recovering from the precipitous decline that oc-

[7] Fritz, L. W. 1993. Trawl locations of walleye pollock and Atka mackerel fisheries in the Bering Sea, Aleutian Islands and Gulf of Alaska from 1977–92. U.S. Dep. Commer., AFSC Processed Report 93-08, 162 p.

[8] Nunnallee, E. P. 1991. An investigation of the avoidance reactions of Pacific whiting (*Merluccius productus*) to demersal and midwater trawl gear. ICES C.M. 1991/B:5, 16 p. [Available from Alaska Fisheries Science Center, NMFS/NOAA, 7600 Sand Point Way NE, Seattle, WA 98115.]

[9] Hollowed, A. B., C. Wilson, M. Shima, and P. Walline. 2001. Study to determine the effect of commercial fishing on walleye pollock distribution and abundance. *In* Steller sea lion investigations, 2000 (B. S. Fadely, ed.), p. 89–104. U.S. Dep. of Commer., NOAA, NMFS, AFSC Processed Report 2001-05.

[10] NMFS (National Marine Fisheries Service). 1995. Status review of the United States Steller sea lion, *Eumetopias jubatus*, population. National Marine Mammal Laboratory, Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA 98115, 61 p.

curred in the 1980s. However, it is important to keep in mind that pollock are only one component of the Steller sea lion diet and that all pollock survey data are collected during the summer.

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Movements of bocaccio (*Sebastes paucispinis*) and greenspotted (*S. chlorostictus*) rockfishes in a Monterey submarine canyon: implications for the design of marine reserves

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Abstract—In August and September of 1997 and 1998, we used SCUBA techniques to surgically implant Vemco V16 series acoustic transmitters in 6 greenspotted rockfish (*Sebastes chlorostictus*) and 16 bocaccio (*S. paucispinis*) on the flank of Soquel Canyon in Monterey Bay, California. Fish were captured at depths of 100–200 m and reeled up to a depth of approximately 20 m, where a team of SCUBA divers anesthetized and surgically implanted acoustic transmitters in them. Tagged fish were released on the seafloor at the location of catch. An array of recording receivers on the seafloor enabled the tracking of horizontal and vertical fish movements for a three-month period. Greenspotted rockfish tagged in 1997 exhibited almost no vertical movement and showed limited horizontal movement. Two of these tagged fish spent more than 90% of the time in a 0.58-km^2 area. Three other tagged greenspotted rockfish spent more than 60% of the time in a 1.6-km^2 area but displayed frequent horizontal movements of at least 3 km. Bocaccio exhibited somewhat greater movements. Of the 16 bocaccio tagged in 1998, 10 spent less than 10% of the time in the approximately 12-km^2 study area. One fish stayed in the study area for about 50% of the study time. Signals from the remaining 5 fish were recorded in the study area the entire time. Bocaccio frequently moved vertically 10–20 m and occasionally displayed vertical movements of 100 m or greater.

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Fish. Bull. 100:324–337 (2002).

Rockfishes (*Sebastes* spp.) are an important component of the commercial and recreational fisheries on the U.S. west coast. Recent stock assessments conducted by the Pacific Fishery Management Council (PFMC) have indicated large population declines for several species of rockfishes (PFMC[1]). For example, bocaccio (*Sebastes paucispinis*) abundance was estimated by MacCall et al.[2] to be 2–4% of pre-harvest levels, causing bocaccio to be formally designated as overfished by the U.S. National Marine Fisheries Service. This severe population decline prompted conservation organizations such as the World Conservation Union to consider bocaccio to be at high risk of extinction (IUCN, 1996). Even as management regulations have become more stringent, however, bocaccio populations continue to decline (MacCall et al.[2]).

As a result of these population declines, new management techniques, such as marine reserves, have been contemplated for west coast rockfishes (Yoklavich, 1998). Marine reserves currently are being considered as supplements to traditional fishery management schemes in many places around the world (Agardy, 1997; Allison et al., 1998). Marine reserves can serve as undisturbed areas for research, as regions designated for limited harvest, or as fishery exclusion zones where fishes can take refuge from exploitation (Murray et al., 1999). They also can serve as a buffer for management trials and as sources for recruits to fisheries (Johnson et al., 1999; Nowlis and Roberts, 1999). The effectiveness of marine reserves for conservation of heavily fished species, however, is dependent upon the size, shape, and location of reserves and on rates of movement of the protected species (Polacheck, 1990; DeMartini, 1993; Lauck et al., 1998). In this respect, an understanding of the rates and directions of daily movements of rockfishes is vital to understanding the value of marine reserves for these species (Carr et al., 1998; Starr, 1998).

[1] PFMC (Pacific Fishery Management Council). 1999. Status of the Pacific coast groundfish fishery through 1999 and recommended acceptable biological catches for 2000: stock assessment and fishery evaluation. Pacific Fishery Management Council, 2130 SW Fifth Avenue, Suite 224, Portland, OR.

[2] MacCall, A. D., S. Ralston, D. Pearson, and E. Williams. 1999. Status of bocaccio off California in 1999 and outlook for the next millenium. *In* Appendix: status of the Pacific coast groundfish fishery through 1999 and recommended acceptable biological catches for 2000: stock assessment and fishery evaluation. Pacific Fishery Management Council, 2130 SW Fifth Avenue, Suite 224, Portland, OR.

Few studies have described the movements of commercially caught rockfishes in water deeper than 100 m, however, because of the difficulty in achieving high survival rates for fish tagged at those depths. Most rockfishes have physoclistous swim bladders that expand with the reduced pressure as these fish are brought to the surface. The resulting barotrauma causes death for almost all fish when captured from waters deeper than 20–30 m, rendering traditional tagging techniques ineffective.

We developed techniques to surgically implant sonic transmitters at depth, thus reducing tagging mortality (Starr et al., 2000). These techniques enabled us to estimate the movements of two rockfishes with different life history characteristics. In 1997, we placed sonic transmitters in six greenspotted (*S. chlorostictus*) rockfish, a species presumed to be relatively sedentary (Yoklavich et al., 2000). In 1998, we tagged 16 bocaccio, a more mobile species (Love, 1996). In both years, we tracked the horizontal and vertical movements of tagged fish for a three-month period.

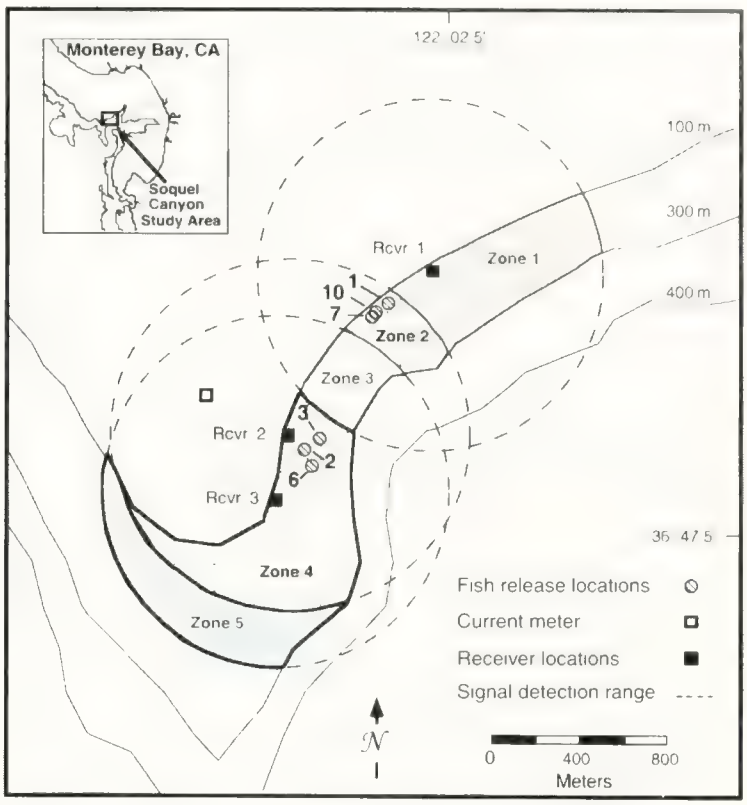

Figure 1

Fish-release locations and tag numbers, receiver locations, current meter location, expected signal detection range, and resulting receiving zones for the 1997 study of greenspotted rockfish.

Materials and methods

Field procedures

Our study site was located on the flank of the submerged Soquel Canyon in 100–250 m of water, approximately 20 km off shore in Monterey Bay, California (Fig. 1). Soquel Canyon contains steep sediment slopes and rock walls interspersed with 50–100 m wide benches, comprising soft sediment and rock outcrops (Yoklavich et al., 2000). Several of the rock outcrops located at the rim of the canyon are 10–20 m high by 50–100 m long scarps with boulders at the bases of the linear rock walls.

In 1997, we caught greenspotted rockfish using longline fishing gear deployed from a research vessel. In 1998, we hired a commercial fisherman to catch bocaccio using modified trolling gear. In both years, fishing lines were retrieved at about 20 m/min. Fishes were brought to a depth of about 20 m and held there for tagging. Divers then surgically implanted Vemco V16 (Vemco Ltd., Nova Scotia, Canada) sonic tags into the captured fish. Following surgery, tagged fish were placed in a recovery-release cage, then towed to the differential GPS location at which they were caught, whereupon the cage was lowered to the seafloor and fish were released. We used the *Delta* submersible to verify that tagged fish were alive after release. A more complete description of tagging and underwater tracking procedures is provided in Starr et al. (2000).

Vemco VR-20 receivers were moored on the seafloor for the duration of the study as a means of tracking tagged fish. The positions of receiver deployment spanned the distribution of release locations of the tagged fish. To increase the amount of positional information available from the receiver data, we placed the tagged fish and receivers along the side of a submarine canyon that stretched northeast to southwest. On 7 October 1997, we placed three receivers on a ledge at a depth of about 160 m along the wall of the canyon (Fig. 1). The receivers spanned a distance of 1500 m and recorded signals for 6 minutes out of every half-hour. We retrieved them on 5 January 1998.

In 1998, we deployed two receivers on surface buoys from 17 August through 10 September because tagging operations commenced one month before the submersible was scheduled to deploy the underwater moorings. These receivers were placed near the locations at which fish were released, in the northeastern portion of the Soquel Canyon study area (site 1, Fig. 2) and in the southwestern portion of the study area (site 2, Fig. 2). On 16 September 1998, we placed six receivers at various depths about 1000 m apart (Fig. 2) and retrieved them on 30 December 1998. Two of the receivers were located in about 100 m of water on the relatively flat substrate above the canyon rim. The other four receivers were placed in deeper water on flat benches or gently sloping walls below the canyon rim. These receivers recorded signals for 12 minutes every hour. In both years, battery life of the tags exceeded the length of time the receivers were moored.

Signal detection range of the moored receivers was about 800 m (Starr et al. 2000). Thus, if a signal was recorded at a particular time by only one receiver, we knew

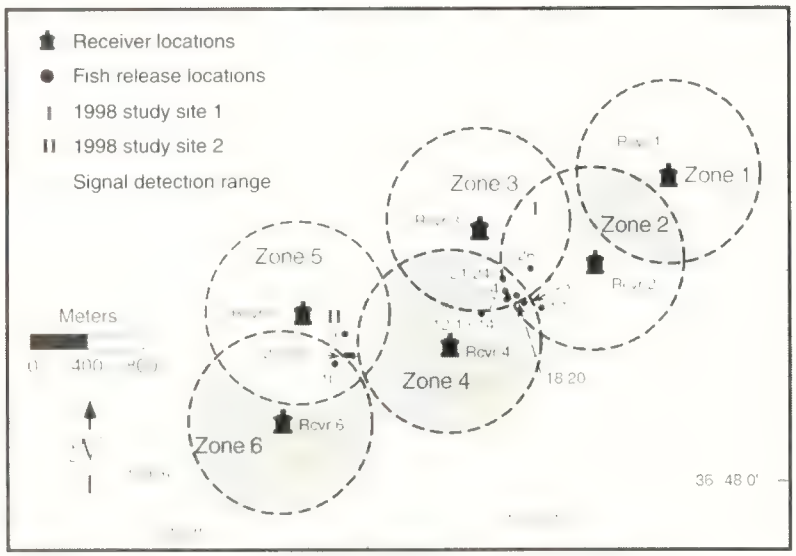

Figure 2

Fish-release locations with tag numbers, receiver locations, current meter location (moored with receiver 1), expected signal detection range, and resulting receiving zones for the 1998 field study of bocaccio.

Table 1

Patterns of signal receptions that define "receiving zones." Signals recorded concurently by the listed combinations of receivers were assigned a receiving zone that represents an approximate location of a tagged fish in a specified time period.

1997		1998	
Receivers (by receiver number) that recorded signals	Receiving zone no.	Receivers (by receiver number) that recorded signals	Receiving zone no.
1	1	1	1
1,2	2	1,2	2
2	3	2	3
2,3	4	2,3	3
3	5	2,3,4	3
		2,4	3
		3	3
		3,4	4
		4	4
		4,5	5
		5	5
		5,6	5
		6	6

the tag was located within 800 m of that receiver and outside the range of detection of other receivers. If a signal was recorded at the same time by two or more receivers, we knew the tag was somewhere within the intersection of the circles that represented the overlap of detection range for the respective receivers. We defined the combinations of intersections or exclusions of overlapping 800-m detection ranges as "receiving zones." In 1997, five such receiving zones were detected (Table 1). We labeled the northeasternmost receiving zone (signals only recorded by receiver 1) as zone 1. Zone numbers increased to the southwest. Because we knew the depths of all the greenspotted rockfish tracked in 1997, we were able to refine estimated locations of a tag to the area in each receiving zone that was between the 100–300 m isobaths (Fig. 1).

In 1998, the same method provided 13 combinations of overlapping detection ranges—too many to permit the patterns of fish movement to be understood easily. Consequently, we grouped combinations of overlapping detection ranges into six receiving zones by their spatial distribution

(Table 1). This enabled us to use signal location and tag depth data to more effectively estimate fish positions and movements. Again, the most northeastern receiving zone (signals only recorded by receiver 1) was labeled as zone 1; zone numbers increased to the southwest (Table 1, Fig. 2).

Each year we placed an S-4 current meter with recording thermometer and salinometer on a mooring near the seafloor to determine if changes in current, salinity, or temperature affected fish movement. In 1997, the current meter was located in 100 m of water on the shelf about 400 m away from receiver 2 (Fig. 1). In 1998, the current meter was moored with receiver 1, and was located in 100 m of water (Fig. 2).

Data analysis

Receivers logged the tag number, date, time of day, acoustic frequency, and tag depth each time a signal was detected. Receivers also recorded signal strength, noise, gain, and error messages provided by the receiver software. Data collected by the moored receivers were downloaded as text files and imported into a database for analysis. Tag depth was plotted versus time of signal reception for each tag and each receiver. Differences in fish depths by time of day were analyzed with ANOVA and Scheffe's *F*-test *post-hoc* analysis (Sokal and Rohlf, 1997).

In 1997, we grouped signals into half-hour time intervals to compare signal receptions between receivers. In 1998, we grouped signals into hourly intervals. We labeled each interval a time "bin" and standardized bin numbers among all receivers. Thus, any signal recorded by a receiver in a given time period (bin) could be directly compared with signals from other receivers in similar time bins. In 1997, the study included 4309 half-hour time bins. In 1998, the study included 2535 hourly time bins.

Each signal was thus assigned a time bin and a receiving zone according to the time interval of signal reception and the combination of receivers recording signals from that tag number. Treating each receiving zone number as a numeric rank enabled us to use a simple average of rank to identify the predominant receiving zone that a fish occupied in the time bins that occurred during a week (336 weekly bins in 1997 and 118 weekly bins in 1998). A difference in average ranking among weeks indicated the fish had moved; the value of the average indicated the direction in which the fish moved. For each tag, a chi-square test of heterogeneity was used to test for differences in average ranking among weeks. In 1997, week 2 of the study was the first week for which there were transmissions from all tagged fish; thus week 2 was used to represent the expected fish distribution by receiving zone for the chi-square test. In 1998, we used week 1 to represent the expected distribution. We also used the unplanned test of homogeneity of replicates tested for goodness of fit (Sokal and Rohlf, 1997) to determine if the average location of a fish (average rank) was similar between weeks. This method enabled us to group weeks in which a fish was in a similar location. In addition to generating weekly distributions, we used the ranking system to plot semihourly (1997) or hourly (1998) movements of tagged fish.

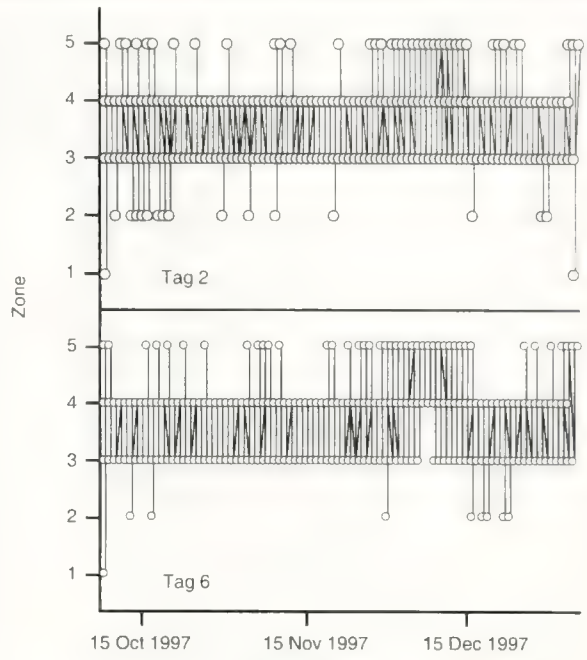

Figure 3

Movements of tagged greenspotted rockfish (tag-2 and tag-6 fish) across study area in 1997, as depicted by changes in receiving zones that were derived from patterns of signal receptions.

Results

Greenspotted rockfish

In 1997, we tagged six greenspotted rockfish, ranging in total length from 35 to 39 cm (Starr et al., 2000). Lea et al. (1999) reported that greenspotted rockfish in this size range are 11–15 yr old and probably mature. The three moored receivers recorded signals throughout the study period from all tags except tag 1. Signals from tag 1 were recorded for 18 hours, then not again until 67 days later. The total number of transmissions recorded from each tagged fish ranged from 156 to 24,132 (Starr et al., 2000).

Except for tag-1 fish, tagged greenspotted rockfish exhibited two patterns of relatively small horizontal movements. Tag-2 and tag-6 fish remained primarily in the receiving zone in which they were released (zone 4) and exhibited few cross-zone movements (Fig. 3, Table 2). Receivers recorded transmissions from each of these tags in 99% of the time bins. More than 56% of the time, signals originated in receiving zone 4, and 94% of the time signals originated from receiving zones 3 or 4 (Table 2), an area comprising 58 ha, or a linear distance along a ledge of 1200 m. When the fish moved out of zones 3 or 4, they most often moved southwest, towards the mouth of Soquel Canyon (towards Zone 5 in Fig. 3). Chi-square and *post-hoc* analyses indicated similarity in the pattern of signals received from the tags for most weeks, as indicated by the weekly average rank of receiving zone (Fig. 4).

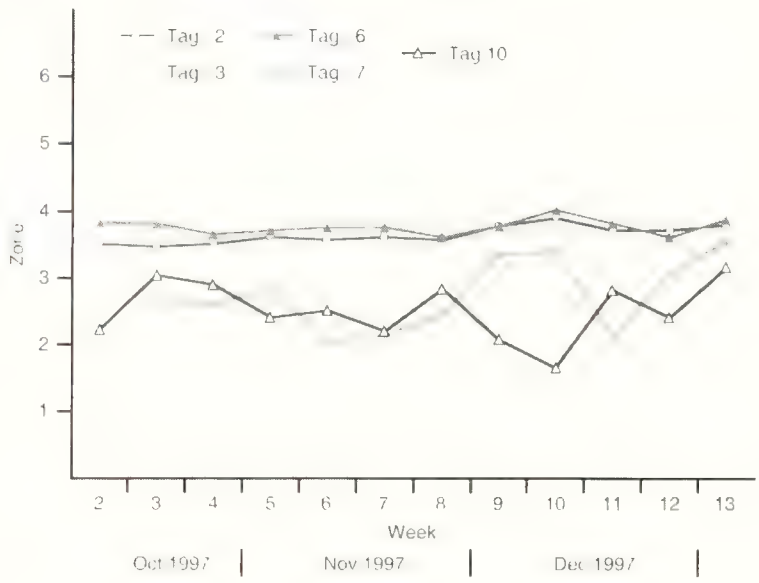

Figure 4

Distribution of tagged greenspotted rockfish in 1997 as depicted by the weekly average rank calculated from receiving zones which were derived from patterns of signal receptions.

Table 2

Percentage of half-hour time bins by receiving zone in which signals were recorded from tagged greenspotted rockfish from 7 October 1997 through 5 January 1998. None = the percentage of time bins in which no signal was recorded.

	Zone number					
Tag number	1	2	3	4	5	None
1	0.1	0.2	0.4	0.3	0.1	98.8
2	0.0	0.4	37.9	56.2	4.4	1.0
3	2.0	3.6	26.5	28.2	14.1	25.6
6	0.0	0.2	26.4	67.3	5.1	1.0
7	11.6	9.6	24.2	8.1	5.2	41.2
10	11.2	12.7	31.6	6.9	2.6	35.0
Zone area (ha)	53.3	11.4	3.9	54.0	36.4	

Table 3

Frequency of time lapse between signals after a time bin in which no receivers recorded signals from tagged greenspotted rockfish in 1997. NA = no signal was recorded for 67 days.

Tag number	0–1 h	1–5 h	5–10 h	>10 h	Max. time (h)
1	NA	NA	NA	NA	
2	7	1	0	0	1.5[1]
3	368	102	7	2	12.5[1]
6	6	0	0	0	1[1]
7	253	107	14	16	30
10	296	101	19	6	27.5

[1] Signals from these fish were not recorded for the first 17 h that receivers were in place and are not included in this table. Signals may not have been recorded because of electronic interference from boats in the area that prevented receivers from recording signals. The other two fish (tag-7 and tag-10 fish) were released a week after receivers were in place.

Tag-3, tag-7, and tag-10 fish moved greater distances, and made relatively frequent short-term movements out of the zone in which they were originally tagged and released (Fig. 5, Table 2). For these tags, 26–41% of the time bins contained no signals. The maximum time recorded for a tag in a single receiving zone was 32% of the time bins, and at least three zones were needed to account for 60% of the signals received from each tag. All three tagged fish showed evidence of moving across the entire study zone, a linear distance of 2940 m, and an area of about 1.6 km^2. Chi-square and *post-hoc* analyses indicated there were significant (P<0.05) differences in the weekly average rank of receiving zone for tags 3, 7, and 10 (Fig. 4). Transmissions from these tags were frequently recorded in all receiving zones (Fig. 5) and the fish also moved out of the study area for short time periods. The maximum time between recorded signals from any of these tags was 30 h. More than 90% of the time, the interval between recorded signals was 5 hours or less (Table 3).

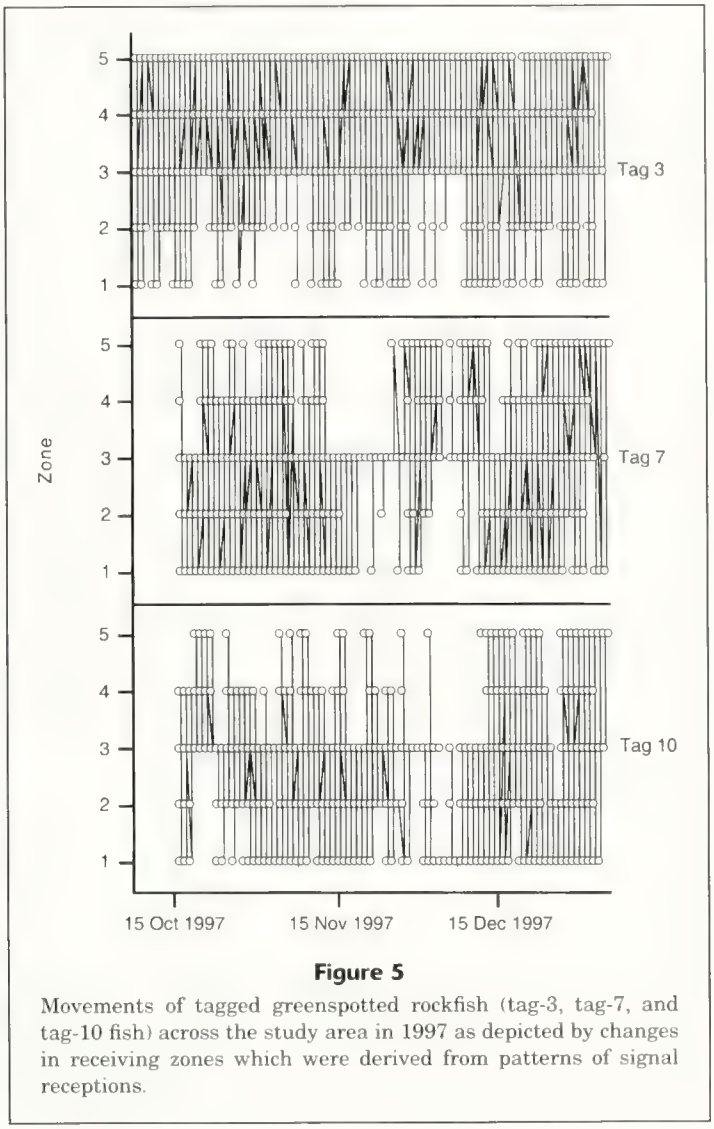

Figure 5

Movements of tagged greenspotted rockfish (tag-3, tag-7, and tag-10 fish) across the study area in 1997 as depicted by changes in receiving zones which were derived from patterns of signal receptions.

All tagged greenspotted rockfish, except tag-1 fish, showed little vertical movement, and 99% of depth transmissions from each tag were within ±3 m (see Fig. 6 for an example of this pattern). This distance is effectively the range of tidal variation and the error associated with the depth sensors in the sonic tags. Some of the fish occasionally made short-term movements to deeper locations. The only exception to this pattern was tag-1 fish that was tracked for 18 hours, lost, then heard again 67 days later. It exhibited vertical movements of about 90 m in the hours before it left the study area (Fig. 7).

Bocaccio

In 1998 we tagged 16 bocaccio, ranging in length from 35 to 58 cm (Starr et al., 2000). Ten of the bocaccio we tagged were larger than the size at 50% maturity reported by Gunderson et al. (1980). The receivers placed on surface buoys in August and early September recorded continuously; the total number of transmissions recorded from each of the tags in that time bin ranged from 0 to 9531 (Starr et al., 2000). The total number of signals recorded by the six subsurface receivers that were deployed from 16 September through 30 December ranged from 0 to 19,213 (Starr et al., 2000). Ten of the tagged bocaccio spent little time in the 12-km^2 study area (Fig. 8). Signals from three tags were recorded only within a few days after tagging and were not heard again (tags 13, 24, 26), either because the fish left the study area or the tags failed to send signals. Lengths of these fish ranged from 47 to 51 cm (Starr et al., 2000). Transmissions from five tags were recorded in the study area for only 1–4 weeks (tags 3, 4, 10, 12, 21). Lengths of these tagged fish ranged from 35 to 52 cm. Three fish appeared to leave the study area and return two weeks to a month later (tags 17, 20, 25). Lengths of these fish ranged from 45 to 55 cm. Signals from the remaining five tags (tags 7, 9, 14, 18, 27) were recorded in the study area the entire time. Lengths of these fish ranged from 47 to 58 cm.

Signals from 10 tags were recorded in less than 10% of the time bins in any zone (Table 4). Signals from one tag

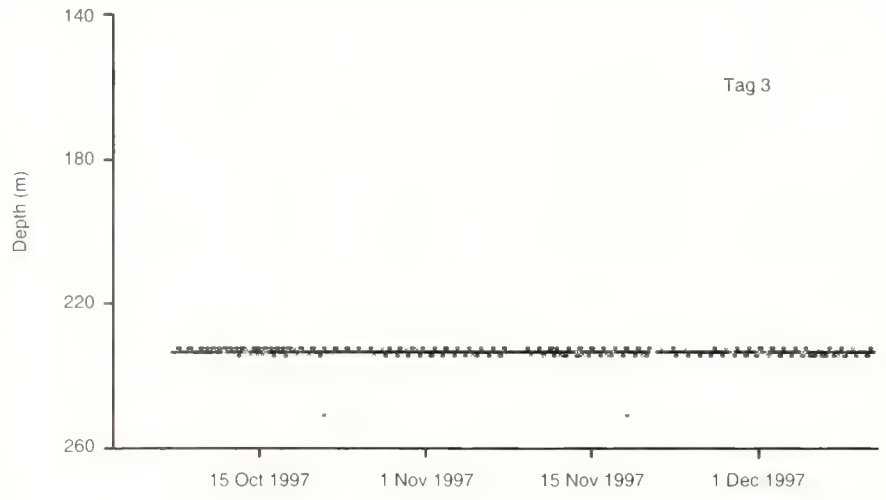

Figure 6

Depth distribution of signals received from tag 3 in 1997. Tag 3 is presented as an example of the depth distributions observed from all tagged greenspotted rockfish, except those of tag 1

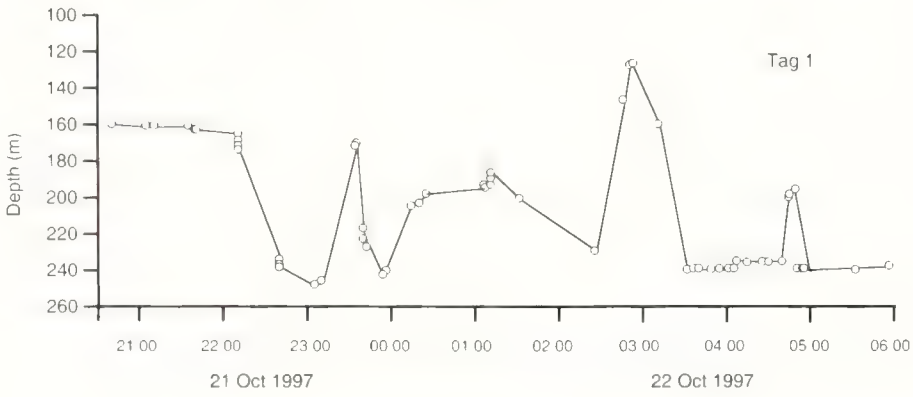

Figure 7

Depth distribution of signals received from tag-1 greenspotted rockfish in 1997

were recorded about 50% of the time, and transmissions from the remaining five tags were recorded in more than 80% of the time bins. The six fish that remained in the study area 50% of the time or more stayed in a small part of the study area (Table 4). Signals from each of four tags (tags 9, 14, 17, 27) were recorded almost exclusively only where they were released, in receiving zones 4 or 5. These receiving zones comprised an area of 168 ha and 201 ha, respectively. Signals from the other two fish (i.e. tags 7, 18) were recorded primarily in receiving zones 3 and 4, an area of about 400 ha. Chi-square and *post-hoc* analyses indicated all fish stayed primarily in the same receiving zones for the time they were in the study area (Fig. 9).

Although the six fish that stayed in the study area stayed primarily in one or two receiving zones, they often exhibited small movements. Plots of zone numbers of recorded signals indicated that two of the fish (tags 7, 18) frequently moved across all receiving zones (Fig. 10). Additionally, cross-talk from receivers 5 and 6 indicated that tag-27 fish made frequent short-term movements (Starr et al., 2000). Tagged fish also occasionally left the study area. Except for tag 17, which was not recorded in the study area for 27 days, the maximum time interval between recorded signals from any of these tags was 57 h. More than 90% of the time, the interval between recorded signals was 5 h or less (Table 5).

Eight of the 16 tags transmitted information about depth. We recorded signals from five of the eight tags for only short time periods after the fish were released. Two of these five fish (tag-3 and tag-12 fish) moved vertically to within 15 m of the surface 9–12 hours after tagging, then returned below a depth of 90 m for a 12–15 day period before signals were lost (see Fig. 11 for an example of tag-3 fish movements). A third fish (tag-4 fish) fluctuated ±10 m around a depth of 90 m for a week, moved vertically to a depth of 14 m, and returned to a depth of about 90 m for another three weeks before signals ceased. A fourth tag (tag 13) was recorded for 3 days and exhibited frequent fluctuations of 20 m in depth before signals ceased.

Data from the remaining three fish containing depth transmitters were recorded throughout the study. Depth transmissions from tag 14 varied less than 3 m, whereas depth transmissions from tag 7 (Fig. 12) and tag 9 (Fig. 13) indicated cyclical vertical movements of ±10–20 m, and occasional deeper dives. The greatest variation in depth was exhibited from tag 7. That fish made several dives of 100 m; once it moved from 100 m to 220 m and back in a 20-h period. Tag-7 and tag-9 fish also demonstrated a diurnal periodicity in vertical movements. Fish were more active and higher during the day and less active and deeper at night (Fig. 14). The ANOVA and Scheffe's *F* test statistics indicated significant differences in both depth and change in depth between dawn, day, dusk, and night hours (Table 6).

Environmental parameters fluctuated but did not appear to be related to fish movements. Salinity and temperature data from the S-4 current meter at 100-m depth fluctuated within 24-h periods, but there were no obvious trends within or between years. Salinity averaged 33 ppt in 1997 and 34.5 ppt in 1998. Water temperature fluctuated from 10 to 15°C in 1997, whereas in 1998 it was more consistent, ranging from 9 to 11°C. Current speed and direction fluctuated in what appeared to be a tidal basis (Shea and Broenkow, 1982), but since there was no obvious relationship to recorded movements, this relationship was not explored in more detail.

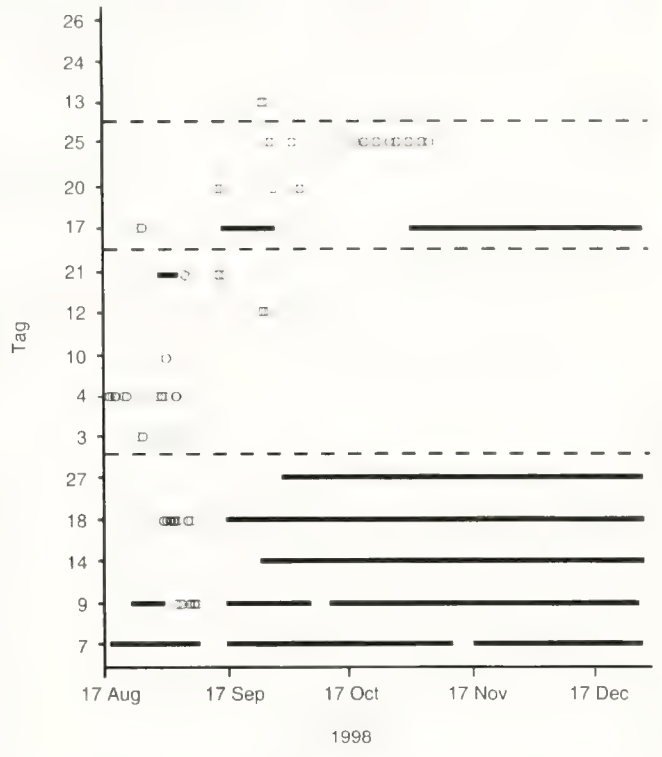

Figure 8

Dates of signal receptions in study area from sonic transmitters implanted in bocaccio in 1998. Circles represent individual occurrences of recorded signals; solid lines represent almost continuous occurrences of recorded signals. Dashed lines on the graph are shown to separate the groups of tagged fish discussed in the text.

Discussion

Fish movements

The *in situ* tagging procedures we developed alleviated many problems associated with surface tagging and provided means for tracking deeper-water rockfishes. We expected greenspotted rockfish to move only small distances because of their affinity to seafloor habitats such as overhangs and crevices (Stein et al., 1992; Yoklavich et al., 2000). Our work confirmed that greenspotted rockfish are relatively sedentary. The greenspotted rockfish we tagged with depth transmitters moved less than ±3 m vertically during the study, except for a few occasions when a fish swam down 20–40 m, only to return to its original depth within 2 hours. This small variation in depth displayed by the tagged greenspotted rockfish indicated that these fish most likely do not leave canyon wall habitats to feed. Love (1996) indicated that they eat mainly small invertebrates, but also cephalopods and fishes. It is possible that prey in the water column is advected toward them along the canyon wall (Isaacs and Schwartzlose, 1965; Genin et al., 1988). They do not appear to migrate vertically to feed on scattering layer organisms as do other rockfishes such as yellowtail rockfish (*Sebastes flavidus*) off Oregon (Pereyra et al., 1969).

Horizontal movements of the tagged greenspotted rockfish were on the order of hundreds of meters to a few kilometers. Receivers 2 and 3 each recorded cross-talk from signals of the same two tags (tags 2, 6) at several different times, indicating that these fish alternately swam close to one receiver, then at a later time swam close to a second receiver that was more than 300 m away (Starr et al., 2000). Although most movements were contained well within the 3-km long study area, half of the fish made sojourns out of the study area for short time periods. We think these small, short-term movements represent foraging activity along the canyon ledge.

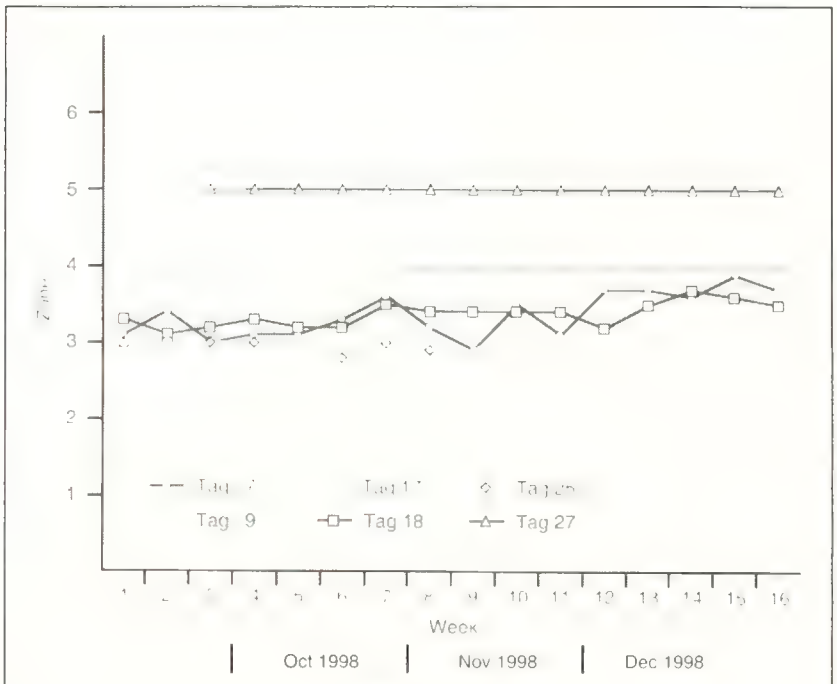

Figure 9

Distribution of six tagged bocaccio in 1998 as depicted by the weekly average rank calculated from receiving zones derived from patterns of signal receptions.

Table 4

Percentage of hourly receiving bins in which signals from tagged bocaccio were recorded from 16 September through 30 December 1998. None = the percentage of time bins in which no signal was recorded.

Tag number	Zone number						None
	1	2	3	4	5	6	
3	0.0	0.0	0.0	0.0	0.0	0.0	100.0
4	0.0	0.0	0.0	0.0	0.0	0.0	100.0
7	3.3	3.8	41.5	35.3	1.7	0.7	13.7
9	0.0	0.0	0.0	0.2	67.5	17.6	14.7
10	0.0	0.0	0.0	0.0	0.0	0.0	100.0
12	0.0	0.0	0.2	0.4	0.1	0.1	99.2
13	0.0	0.0	0.2	0.4	0.1	0.1	99.2
14	0.0	0.0	0.1	98.0	0.5	0.0	1.4
17	0.0	0.0	0.0	50.4	0.0	0.0	49.6
18	2.0	8.7	29.6	39.3	2.0	0.0	18.4
20	0.0	0.0	0.2	0.0	0.5	0.1	99.3
21	0.0	0.0	0.4	0.4	1.3	0.0	97.9
24	0.0	0.0	0.0	0.0	0.1	0.0	99.9
25	0.3	0.0	5.1	0.0	0.0	0.0	94.7
26	0.0	0.0	0.0	0.0	0.0	0.0	100.0
27	0.0	0.0	0.0	0.0	99.7	0.0	0.3
Zone area (ha)	124.0	75.5	232.2	168.0	201.0	132.4	

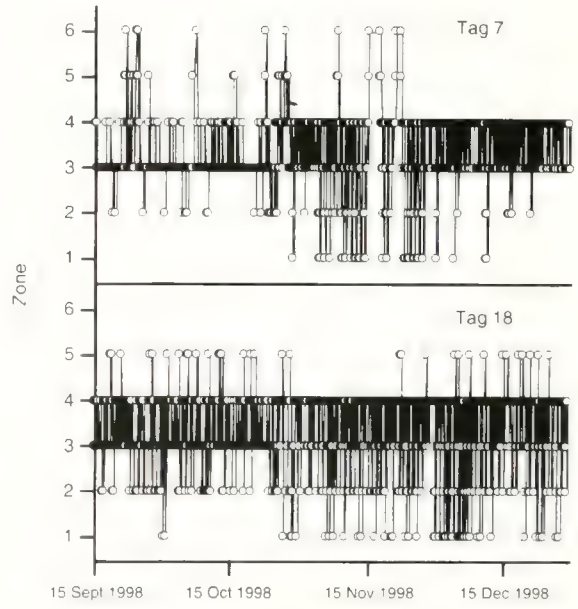

Figure 10

Movements of tag-7 and tag-18 bocaccio across the study area in 1998 as depicted by changes in receiving zones derived from patterns of signal receptions.

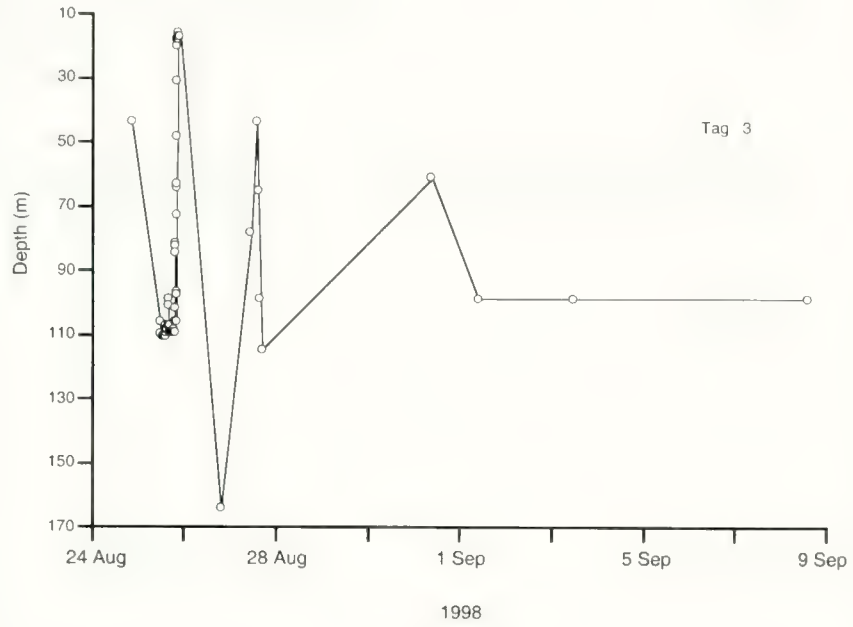

Figure 11

Depth distribution of signals received from tag-3 bocaccio in 1998. Tag-12 bocaccio displayed a similar pattern.

We expected bocaccio to move more than greenspotted rockfish. Bocaccio are frequently caught in midwater trawl nets and are considered more mobile than greenspotted rockfish (Love, 1996). Hartman (1987) reported that juvenile bocaccio moved a maximum of 148 km over two years in tag-recapture studies in southern California. In this respect, young bocaccio are similar to yellowtail rockfish (*Sebastes flavidus*) that have exhibited movements on the scale of hundreds of kilometers in tag-recapture studies conducted in Alaska and British Columbia (Stanley et al., 1994). In Stanley et al.'s studies, 75% of the tag recoveries were within 25 km of the release point, but maximum movement observed was 250 km for Canadian yellowtail rockfish, and 1400 km for Alaskan fish.

Not all studies have shown that yellowtail rockfish move great distances, however. Using ultrasonic telemetry, Pearcy (1992) tracked them from the surface intermittently for periods of several days and reported that tagged fish generally stayed within 2 km of the capture or release location. After a period of 13 days in 1990, 11 of 12 tagged fish were detected within 300 m of the capture site, even though some fish had been displaced. A month after release, eight of 12 tagged fish were within 1.4 km of the capture location.

Pearcy (1992) also suggested that the tagged fish exhibited site fidelity to a pinnacle habitat. Pearcy's work, combined with results from other displacement studies (Carlson and Haight, 1972; Hallacher, 1984; Matthews, 1990; Heilprin, 1992), suggests that several species of rockfish possess homing ability. Half of the bocaccio we tagged either stayed in the study area during the entire time of the study, or left and returned, suggesting some site fidelity. Evidence of site fidelity was also provided by the chi-square analyses of fish location in receiving zones. The analyses indicated that bocaccio remained in the same area over the course of a week, despite the evidence of frequent movements out of a receiving zone on a daily basis.

Table 5

Frequency of time lapse between recorded signals after a time bin in which no receivers recorded signals from tagged bocaccio in 1998. Only tagged fish that remained in the study area for more than 50% of the time are shown.

Tag number	0–1 h	1–5 h	5–10 h	>10 h	Max. time (h)
7	115	30	6	3	57
9	152	66	1	2	28
14	14	2	0	0	1
17	143	86	10	5	660
18	201	86	2	1	12
27	2	0	0	0	1

Although our study was designed to evaluate the residence time of bocaccio in a discrete area, and not to quantify the maximum distance bocaccio move, the relatively small percentage of tagged bocaccio that stayed in our 12-km^2 study area during the entire study period indicated that bocaccio may also move large distances. The results of our study tend to reinforce the hypothesis presented

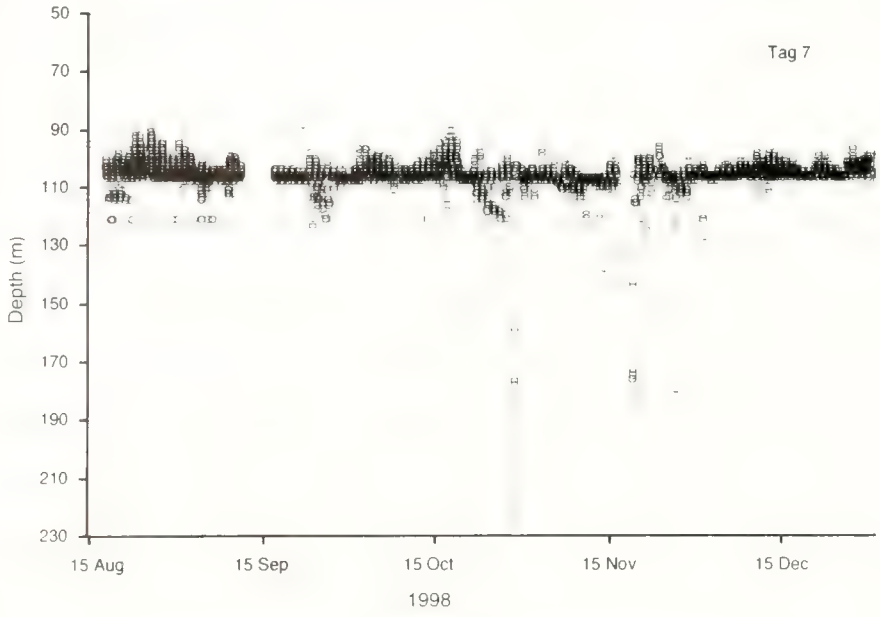

Figure 12
Depth distribution of signals received from tag-7 bocaccio in 1998

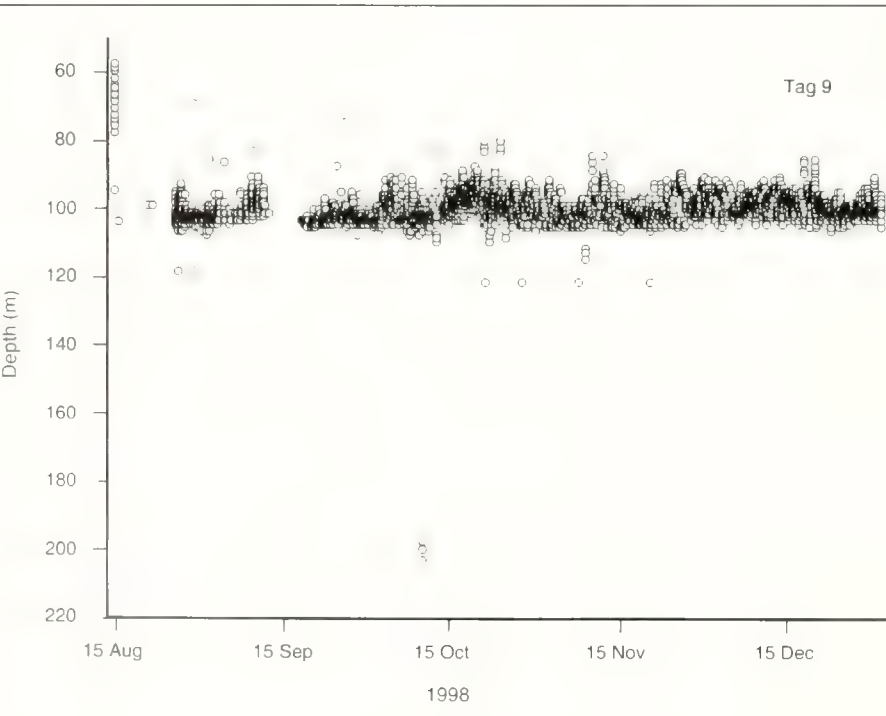

Figure 13
Depth distribution of signals received from tag-9 bocaccio in 1998.

(MacCall[2]) that there are two types of observed movements of bocaccio: pelagic and "refugial." They suggested, from observations of the large sizes of bocaccio observed as single individuals and the occurrence of smaller animals in mid-water trawl catches, that there may be an ontogenic shift from pelagic to refugial habits. They hypothesized

that subadults are more mobile than adults, and as the fish increase in size, they become more sedentary. From tag transmissions and submersible surveys, we observed both pelagic and refugial behavior (about 25% of the tagged animals exhibited refugial behavior). The two largest tagged bocaccio were among the five fish that moved the least. The narrow size range of most of the tagged fish, however, precluded an analysis of movements by fish length.

Tagged bocaccio made frequent small vertical movements that were associated with time of day. The magnitude of the vertical movements matched the vertical relief of the habitats used by tagged fish. During submersible operations, we tracked tagged fish in small schools as they moved along rock scarps that were 10–20 m high and 100–200 m long (Starr et al., 2000). These scarps were often at, or just below, the rim of the submarine canyon. The depth transmissions from tags indicated that fish were at the top or just above the rock habitats during the day, and lower and more sedentary at night. We attribute the increased activity during the day to the fact that bocaccio are visual predators (Love, 1996) and are thus more apt to forage during the day.

Four of the eight fish containing depth transmitters made rapid vertical movements. Three of the bocaccio rose vertically to spend a short time near the surface, then returned to depths from which they came. These fish all remained only a few weeks in the study area. A fourth fish made a deep dive to 220 m and back to 100 m in less than a day (Fig. 12). The purposes of these dives are unknown, but such dives reinforce our observations during tagging operations that bocaccio can modify the volume of air in their swim bladder. Pearcy (1992) observed that yellowtail rockfish also are capable of discharging air from their swim bladders in a relatively short time.

For some tags, there were short time intervals when signals were not recorded. This may have been caused by the canyon topography or by fish behavior. The complex topography of Soquel Canyon and the behavior of the rockfishes may have prevented the receivers from receiving all possible transmissions from tagged fish. The hard, steep walls that undulate along the side of the canyon (Yoklavich et al., 2000) occasionally cause echoes and an original transmission to coincide, thus preventing the receivers from recording a valid signal. Other signal lapses may also have been due to the tendency of rockfish to take shelter under rocks or ledges. From the surface, we occasionally heard weak signals that were unusually high-pitched and that sounded "tinny." We have experienced the same type of reception when tracking shallow-water rockfishes that took shelter under a rock or ledge. Signals return to full strength and timbre when the fish leaves the crevice.

Table 6

Results of Scheffe's *F post-hoc* test (*P* values) were used to identify differences in fish depth between different times of the day (i.e. between dawn and day [dawn–day], dawn and dusk [dawn–dusk], etc.) or diel differences in depth and change in depth of signal receptions from tagged bocaccio (tag-7 and tag-9 fish) in 1998.

	Tag 7		Tag 9	
	Depth	Change in depth	Depth	Change in depth
Dawn–day	0.0097	0.0194	<0.0001	<0.0001
Dawn–dusk	0.2840	0.277	0.0040	0.0004
Dawn–night	0.5045	<0.0001	<0.0001	<0.0001
Day–dusk	0.7455	0.9031	0.7312	0.9998
Day–night	<0.0001	0.0065	0.1010	<0.0001
Dusk–night	0.0007	0.0156	0.0440	<0.0001

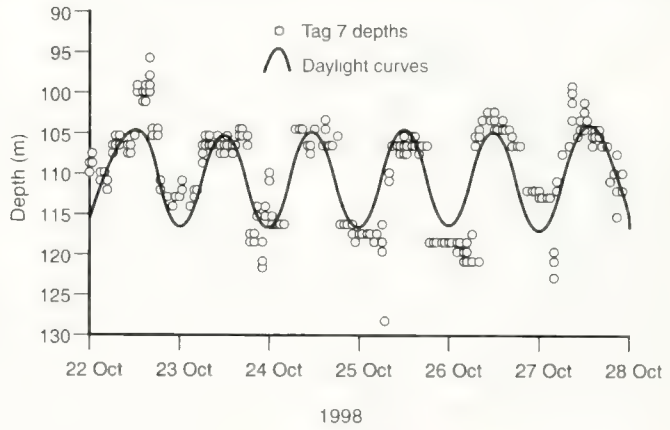

Figure 14

Depth transmissions recorded for tag-7 bocaccio plotted with daylight curve for the period 22–28 October 1998.

Implications for marine reserves

Tag-recapture studies of shallow water (<100 m) demersal rockfishes typically have indicated very little movement; only one species in ten studies exhibited long-term movements greater than 3 km (Stanley et al. 1994; Lea et al., 1999). Results from these studies support the idea that small harvest refugia may effectively protect nearshore rockfishes. This would be fortuitous if almost all nearshore rockfishes have small home ranges, because most of the marine reserves in the eastern Pacific Ocean are very small and have been created without regard to typical movements of species (McArdle, 1997; Starr, 1998; Yoklavich, 1998).

Our results indicate a considerable short-term variation in the movements of individual greenspotted rockfish, which may be masked by the long-term nature of tag-recapture studies. Although almost all fish may remain in a small area over the course of several years, an individual

fish may occasionally move longer distances. This raises a question about the efficacy of marine reserves that are designed to account for modal distributions of fish based on traditional tag-recapture studies.

The efficacy of a marine reserve is directly related to its size and shape and the movements of the protected species (Polacheck, 1990; DeMartini, 1993; Nowlis and Roberts, 1999). Thus, without estimates of both the range and frequency of movements of the target species, it is difficult to predict the effectiveness of a reserve for conserving fishes (Carr and Raimondi, 1998). Infrequent foraging excursions out of a reserve, for example, could potentially negate the value of a reserve if its purpose is to act as a harvest refugium. Conversely, small home ranges could preclude a "spillover" effect and diminish a reserve's ability to enhance local fisheries, if that were the goal. Small reserves may appear to protect species that move little, but if protected fishes occasionally move greater distances, as did the tagged bocaccio and greenspotted rockfishes in our study, then larger reserves may be needed to encompass 90% or more of the typical monthly movements of a species. Models that incorporate movement into the theoretical design and evaluation of marine reserves may thus be strengthened by using the probability or percentage of time an animal actually remains in the reserve boundaries rather than modal distributions. The periodic departure of tagged fish from their center of activity suggests that a conservative strategy for the design of marine reserves would be to include a buffer zone to account for these infrequent sojourns.

Only one-fourth of the tagged bocaccio spent more than 80% of their time in the 12-km^2 study area. Yet the Soquel Canyon study area was two times larger than the mean size and four times larger than 70% of marine reserves in California that regulate fishing in any way (McArdle, 1997). Such movement will require that marine reserves intended to effectively protect bocaccio will need to be much larger than most current reserves. Until the full extent of the range and periodicity of movements is known, however, it will be difficult to adequately design a system of marine reserves to protect bocaccio stocks.

After tagging, greenspotted rockfishes returned to rock habitats on the ledges at the side of Soquel Canyon and exhibited small horizontal and vertical movements. Based on the signal receptions for our three-month period, the size of a marine reserve would need to have a diameter of 3 km to account for 95% of the typical movements of the tagged greenspotted rockfish. Bocaccio, however, returned to higher relief habitats near the canyon rim after release and exhibited much greater horizontal and vertical movements. An effective reserve for bocaccio, therefore, would need to be larger than the 12 km^2 area encompassed by our study.

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Efficiency of bycatch reduction devices in small otter trawls used in the Florida shrimp fishery

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Abstract—Two bycatch reduction devices (BRDs)—the extended mesh funnel (EMF) and the Florida fisheye (FFE)—were evaluated in otter trawls with net mouth circumferences of 14 m, 17 m, and 20 m and total net areas of 45 m^2. Each test net was towed 20 times in parallel with a control net that had the same dimensions and configuration but no BRD. Both BRDs were tested at night during fall 1996 and winter 1997 in Tampa Bay, Florida. Usually, the bycatch was composed principally of finfish (44 species were captured); horseshoe crabs and blue crabs seasonally predominated in some trawls. Ten finfish species composed 92% of the total finfish catch; commercially or recreationally valuable species accounted for 7% of the catch. Mean finfish size in the BRD-equipped nets was usually slightly smaller than that in the control nets. Compared with the corresponding control nets, both biomass and number of finfish were almost always less in the BRD-equipped nets but neither shrimp number nor biomass were significantly reduced. The differences in proportions of both shrimp and finfish catch between the BRD-equipped and control nets varied between seasons and among net sizes, and differences in finfish catch were specific for each BRD type and season. In winter, shrimp catch was highest and size range of shrimp was greater than in fall. Season-specific differences in shrimp catch among the BRD types occurred only in the 14-m, EMF nets. Finfish bycatch species composition was also highly seasonal; each species was captured mainly during only one season. However, regardless of the finfish composition, the shrimp catch was relatively constant. In part as a result of this study, the State of Florida now requires the use of BRDs in state waters.

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Commercial fishermen use a variety of gears to harvest shrimp in southeastern U.S. waters, but they have predominantly used the otter trawl since the 1940s. The otter trawl is an unselective gear that commonly has an associated catch of untargeted organisms (e.g. finfish, miscellaneous invertebrates) that are referred to as "bycatch." Numerous definitions for the term " bycatch" have been proposed (Allsopp, 1982; Caddy, 1982; Saila, 1983). The most comprehensive, suggested by Alverson et al. (1994), refers to nontargeted species retained, sold, or discarded for any reason.

An estimated average of 27.0 million metric tons (t) (range=17.9–39.5 million t) of bycatch are discarded annually by the world's marine fishing fleets (Alverson et al., 1994). Shellfish fisheries compose 14 of the top 20 fisheries worldwide in quantity of bycatch discards (Alverson et al., 1994) and account for 9.5 million t of discards annually. Because the harvest of bycatch often exceeds that of the targeted species, the issue of bycatch in marine fisheries has become a global concern.

In the southeastern United States, the penaeid shrimp fishery often ranks first in value of all fisheries for commercially harvested marine species. In 1996, total landings were 98 million kg and were valued at approximately $434 million, ex-vessel price (size-specific price per unit volume paid to the fisherman for the catch) (NMFS[1]). The Gulf of Mexico (referred to as "Gulf" in this study) shrimp fishery accounted for 90% of this volume and 87% of this value. In U.S. waters, the Gulf and the southeast U.S. Atlantic (referred to as "South Atlantic") shrimp trawl fisheries ranked 5th and 9th, respectively. Their ratios of kg finfish bycatch to kg shrimp were 10.3:1 for the Gulf, and 8.0:1 for the South Atlantic (Alverson et al., 1994). However, the Gulf and South Atlantic Fisheries Development Foundation (GSAFDF[2]) estimated that the ratio of finfish bycatch to shrimp harvest was 4.2:1 for the Gulf shrimp fishery and 2.8:1 for the South Atlantic shrimp fishery. Thus, using the more conservative ratios reported by GSAFDF and the 1996 shrimp landings for the Gulf fishery (88 million kg) and the south Atlantic fishery (9.9 million kg; NMFS[1]), the estimated total finfish bycatch for these two fisheries is 370 million kg and 28 million kg, respectively.

In 1996, approximately 11.3 million kg of shrimp were landed along the Florida Gulf coast and 1.8 million kg of shrimp were landed along the Florida Atlantic coast (NMFS[1]). Ratios of finfish bycatch to shrimp for the Florida Gulf coast ranged from 2.3:1 (fish-

[1] NMFS (National Marine Fisheries Service). 1997. Bycatch in the southeast shrimp trawl fishery. A data summary report. National Marine Fisheries Service, Southeast Science Center, 75 Virginia Beach Drive, Miami, FL 33149. 197 p.

[2] GSAFDF (Gulf and South Atlantic Fisheries Development Foundation). 1997. Bycatch and its reduction in the Gulf of Mexico and South Atlantic shrimp fishery. Final report to the National Oceanic and Atmospheric Administration (award NA57 FF0285). GFSFDF, Suite 997, Lincoln Center, 5401 West Kennedy Boulevard, Tampa, FL 33609. 27 p.

ing depth >10 fathoms [fm]) to 2.5:1 (fishing depth < 10 fm) (NMFS[1]); thus total finfish bycatch can be estimated at 26.0–28.3 million kg for the Florida Gulf shrimp fishery. With the finfish-to-shrimp ratio of of 2.8:1 for the South Atlantic fishery and the current landings information for Florida, the finfish bycatch for the Florida Atlantic shrimp fishery can be estimated at 5.0 million kg. Since 1990, considerable research has been conducted to characterize bycatch composition and to develop methods to reduce bycatch in the Gulf and the South Atlantic shrimp fisheries (Nance, 1992, 1993; GSAFDF[2,3]; Nichols et al.[4]; NMFS[5]). In addition, numerous fishery-independent surveys examining bycatch characterization and the efficiency of bycatch reduction devices (BRDs) have been conducted by state and private organizations throughout the southeastern U.S.A. (Burrage et al.[6]).

In 1990, the Florida Marine Fisheries Commission (FMFC; now Florida Fish and Wildlife Conservation Commission) began to develop a shrimp fishery management plan that included a mandate to reduce the bycatch of total finfish biomass in shrimp trawls by 50%. Responding to this policy decision, a bycatch-characterization study of the inshore Florida shrimp fishery was conducted statewide (Coleman et al.[7]; Coleman et al.[8]). Field studies comparing the efficiencies of two types of BRDs (Florida fish eye [FFE], large-mesh extended-mesh funnel [EMF]) in otter trawls and rollerframe trawls were also conducted (Continental Shelf Associates Inc.[9]; Coleman and Koenig[10]; Coleman et al.[11]).

The issue of bycatch in the Florida shrimp trawl fishery has exacerbated conflicts between conservationists and recreational and commercial fishermen over the allocation of marine resources. Relevant issues include the following: 1) the high mortality rates of economically important juvenile finfish caught in shrimp trawls, which could reduce harvestable finfish stocks; 2) the high mortality rates of nonharvested species caught in shrimp trawls, which could alter the overall health of the marine environment; and 3) the perceived waste of bycatch species that are discarded.

This controversy was partly responsible for the passage of a Florida constitutional amendment (Article X, Section 16) that reduced the size of shrimp trawl nets used in the coastal shrimp fishery to 500 sq. ft. (45 m^2) of mesh area per net and limited the number of nets to two per vessel. In previous studies conducted in Florida to examine the efficiency of BRDs in shrimp trawls (Coleman and Koenig[10]), net sizes greatly exceeding that authorized by the amendment were tested. The goal of our study was to test how efficiently the FFE and EMF excluded finfish in small otter trawls (overall mesh area=45 m^2) of various mouth-perimeter sizes. This information can be used by fisheries managers when considering the use of BRDs in inshore and nearshore shrimp fisheries.

Materials and methods

Tampa Bay is located on the west-central coast of Florida (Fig. 1) and is the largest open-water estuary in the state (Lewis and Estevez, 1988). The bay is a subtropical estuary that has patches of fringing seagrass meadows (Lewis et al., 1981), but fine sand is the predominant seabottom type (Brooks[12]).

Gear specifications

Conventional semiballoon otter trawls (Fig. 2) are used to harvest pink shrimp (*Farfantepenaeus duorarum*) in Tampa Bay. Otter trawls are typically used on unvegetated, sandy-bottom areas. We tested the effectiveness of

[3] GSAFDF (Gulf and South Atlantic Fisheries Development Foundation). 1993. Organization and management of a Gulf of Mexico and south Atlantic Ocean fishery bycatch management program (year 2). Final report to National Marine Fisheries Service (award NA37FD0032). GSAFDF, Suite 997, Lincoln Center, 5401 West Kennedy Boulevard, Tampa, FL 33609, 65 p.

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[9] Continental Shelf Associates, Inc. 1992. Commercial food shrimp fishery impacts on by-catch in the lower St. Johns River, Florida. Draft final report C-7238. Continental Shelf Associates, Inc., 759 Parkway Street, Jupiter, FL 33477, 35 p.

[10] Coleman, F. C., and C. C. Koenig. 1994. Florida inshore shrimping: experimental analysis of bycatch reduction. Final report. National Marine Fisheries Service, MARFIN grant NA37FF0051. Institute for Fishery Resource Ecology, Florida State Univ., Tallahassee, FL 32306, 63 p.

[11] Coleman, F. C., P. Steele, and W. Teehan. 1996. Use of bycatch reduction devices in small trawls of sizes set by the net ban. Final Report. Florida Department of Environmental Protection contract MR081. Florida Dep. Environ. Protection, 100 8th Avenue S.E., St. Petersburg, FL 33701, 75 p.

[12] Brooks, H. K. 1974. Geological oceanography. *In* Summary of knowledge, eastern Gulf of Mexico (J. I Jones, R. R Ring, M. O. Rinkel, and R. E. Smith, eds.), p. IIE1-50. Fla. State Univ. Syst. Inst. Oceanogr., St. Petersburg, FL.

two BRDs, the FFE and the EMF (Fig. 3) in three sizes of otter trawls in Tampa Bay during October–December 1996 (fall) and February–April 1997 (winter). Both BRDs are standard devices that have been recommended by NMFS, are used by the commercial fishing sector, and have been extensively tested in offshore and inshore waters throughout the southeastern United States (Murray et al., 1992; Watson et al., 1993; Rogers et al., 1997; Coleman et al.[7] Christian et al.[13]; McKenna and Monaghan[14]).

The otter trawl dimensions were as follows: 1) 14-m net: mouth circumference = 14.0 m, float-line length = 6.3 m, lead-line length = 6.9 m; 2) 17-m net: mouth circumference = 17.0 m, float-line length = 6.9 m, lead-line length = 7.8 m; 3) 20-m net: mouth circumference = 20.0 m, float-line length = 8.1 m, lead-line length = 9.4 m. The nets were of appropriate lengths to conform to the 45-m^2 total-mesh-area rule. Net perimeters were chosen after consultation with commercial shrimpers and personnel from the NMFS Laboratory Harvesting Section, Pascagoula, Mississippi. All net bodies were constructed of no. 9 twine and had a stretch-mesh size of 3.8 cm; the tailbag was constructed of no. 18 twine and had a stretch-mesh size of 3.2 cm. The FFE was constructed of 13-mm-diameter stainless steel rods. It had an overall length of 30 cm and a 15-cm × 15-cm opening to allow fish to escape. The FFE was mounted at the top center of the tailbag at 70% of the distance between the tie-off rings and the beginning of the codend (Watson et al., 1993; Christian et al.[13]), creating an area of reduced water flow directly behind the FFE, which would allow fish to escape. The EMF had an overall length of 121 cm and a circumference of 120 meshes; it consisted of a web funnel (3.5-cm stretch-mesh size) surrounded by a larger-mesh "escape" section (21-cm stretch-mesh size) held open by a plastic-coated hoop. One side of the funnel was extended to form a lead panel that created an area of reduced water flow on the back side of the funnel, similar to that created by the FFE.

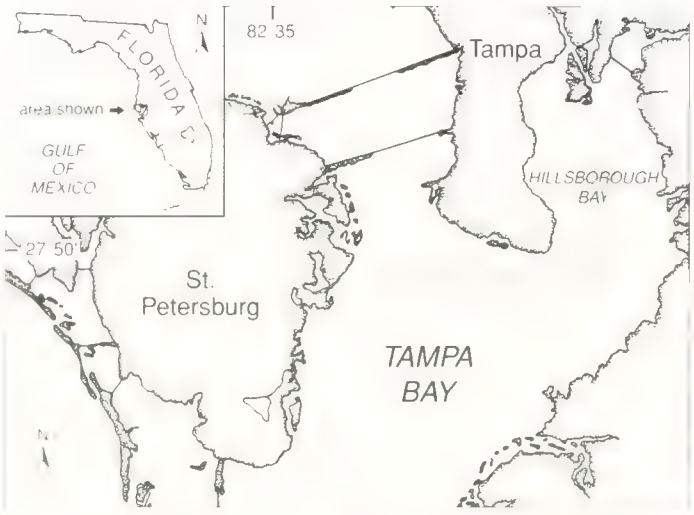

Figure 1

Tampa Bay, Florida. Hatched region shows sampling area.

To conform to federal regulations, each net was equipped with a turtle excluder device (TED) placed near the mouth of the tailbag (Fig. 2). The standard super-shooter TED consisted of a metal grid of seven aluminum bars with a 9-cm interbar distance; the grid was set at a 45° angle to direct turtles downward toward the escape opening (Watson et al., 1993). Sewn in front of the TED was a section of webbing (3.2-cm stretch-mesh) that formed an accelerator funnel (Fig. 3A), which increased the velocity of water and entrained organisms both through the TED and into the net tailbag. The tailbag section and the combined TED and accelerator-funnel section could be zipped to any trawl body, regardless of size. The zipper ensured random pairing of trawl body and tailbag and enabled the experimental and control nets to be easily exchanged throughout the project. The BRDs and TEDs used during this project were approved by the NMFS Laboratory Harvesting Section, Pascagoula, Mississippi.

Both types of BRDs were tested in each net size. For each net size, one net of a matched pair was equipped with either the FFE or the EMF and served as the experimental net and the other, unaltered net served as the control. In the experimental net, the FFE or EMF was installed behind the TED-accelerator funnel section. The net with the BRD was deployed off a randomly chosen side of the boat and its paired control net was deployed simultaneously off the other side in a double-rig trawl towed from 3.5-m outriggers. Each net was spread by two 123-cm × 62-cm wooden trawl doors linked by a tickler chain.

[13] Christian, P. A., D. L. Harrington, D. R. Amos, R. G. Overman, L. G. Parker, and J. B. Rivers. 1993. Final report on the reduction of finfish capture in south Atlantic shrimp trawls. Final report to National Marine Fisheries Service (award NA27FD 0070-01). Univ. Georgia, 715 Bay Street, Brunswick, GA 31520, 83 p.

[14] McKenna, S. A., and J. P Monaghan Jr. 1993. Gear development to reduce bycatch in the North Carolina trawl fisheries. Completion report to Gulf and South Atlantic Fisheries Development Foundation (cooperative agreement NA90AA-H-SK052). North Carolina Div. Mar. Fish., 3441 Arendell Street,Morehead City, NC 28557, 79 p.

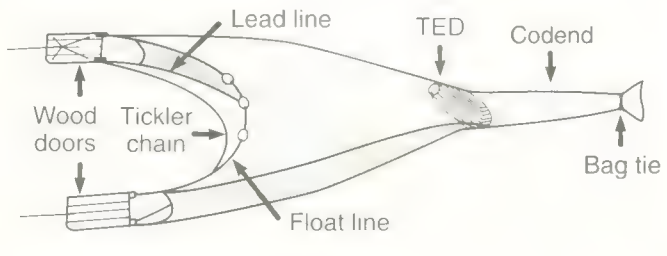

Figure 2

Components of a semiballoon otter trawl equipped with a super shooter turtle excluder device (TED). The TED is required in all shrimp nets in Florida.

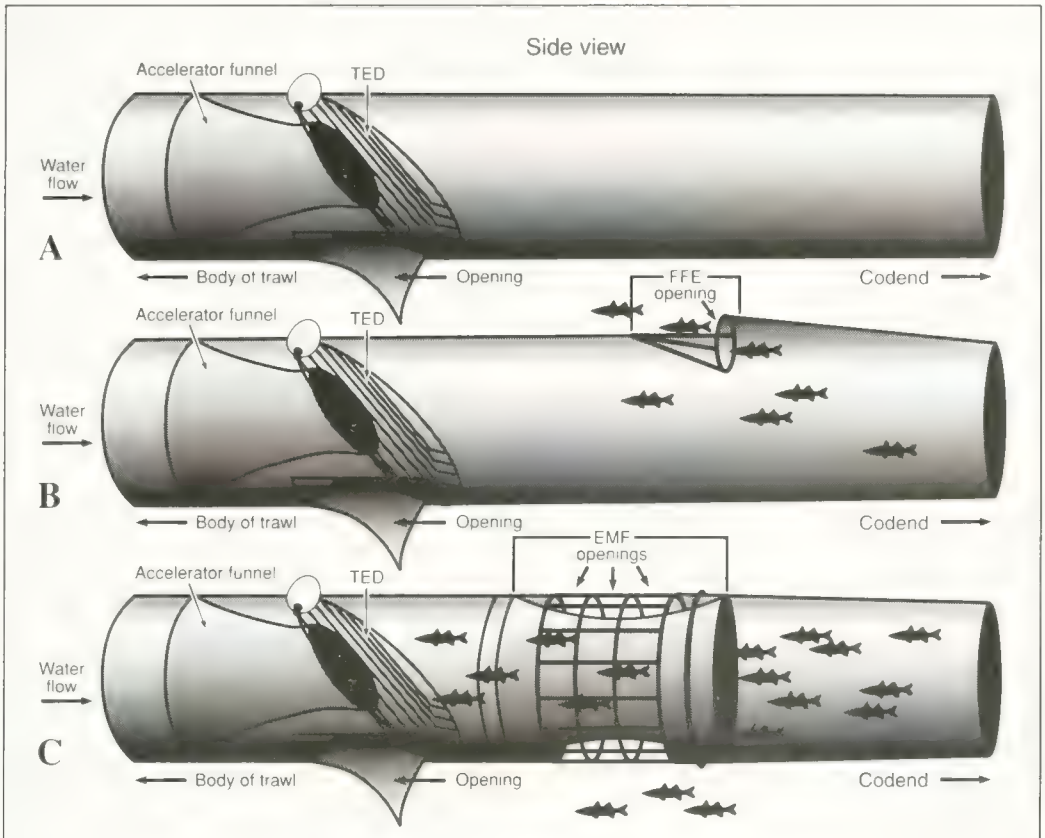

Figure 3

Stylistic diagram of the bycatch reduction devices used in this study: (**A**) Control net equipped with an accelerator funnel in front of the TED; (**B**) net with Florida fisheye (FFE), the device is inserted into the tailbag behind the TED; (**C**) net with large-mesh extended-mesh funnel (EMF) inserted directly behind the TED.

Sampling protocol

Our sampling protocol was established in consultation with representatives from the NMFS Pascagoula Laboratory and the FMFC. Coleman and Koenig[9] established that TEDs did not work as finfish excluder devices in inshore waters; therefore we did not test their exclusion efficiencies.

Sampling was conducted aboard a 35-ft, diesel-powered, Bruno & Stillman trawler boat, modified with outriggers. The nets were deployed and retrieved with a hydraulic powered system. Prior to installing and testing the BRDs, we equipped all pairs of nets of each size with the combined TED and accelerator-funnel sections and tested them for comparable catchability.

To test each BRD type in each size of net, we conducted twenty paired tows at night during a three-week sampling period in each season. Each pair of nets was towed 10 times within a two-week time period. To minimize any potential bias inherent to a particular net or side of the boat, the two nets of each pair were switched to opposite sides of the boat after 10 tows were completed. All paired nets were towed in water depths of 3.5 to 5.0 m for 30-min bottom time at an average speed of 2.5 kn; speed was determined through use of the global positioning system (GPS). All trawling was conducted in areas where the commercial shrimp fishery operates.

The catches from the paired nets (BRD and control) were maintained separately and were sorted onboard the vessel. After each tow, the shrimp, finfish, invertebrates (horseshoe crabs, portunid crabs, sponges, tunicates) and "trash" (seagrass, rocks, shells, anthropogenic debris, etc.) from each net were separated. The large invertebrates (horseshoe crabs, blue crabs, etc.) and trash were weighed separately, the invertebrates were counted, and both the invertebrates and the trash were discarded. The total catch of shrimp and finfish from each net was weighed separately. The shrimp were counted, sex was determined for 10 randomly chosen individuals, and their carapace lengths (CL) were measured to the nearest 0.1 mm. These measurements from the 20 replicate tows were combined to obtain length-frequency distributions for the shrimp. The remaining bycatch, composed of finfish and small invertebrates, was weighed. If the total weight of the bycatch was less than or equal to 4.5 kg, the entire sample was kept; if the weight of the sample exceeded 4.5 kg, a subsample weighing a total of 4.5 kg + 20% of the total bycatch weight was kept. All species of vertebrates and in-

vertebrates from each bycatch sample or subsample were identified; finfish that could not be identified onboard were labeled and returned to the laboratory for identification. All individuals of each finfish species were counted and the finfish bycatch sample or subsample was weighed. To obtain an estimate of the size-frequency distribution for each species of finfish, we measured the standard length (SL) to the nearest 1 mm of 20 randomly selected individuals of each species from each tow and combined the measurements from the 20 replicate tows. If fewer than 20 individuals were caught in a tow, all individuals captured in that tow were measured.

All weights were standardized to grams per minute towed to estimate CPUE (biomass). All counts of individual species were standardized to number per minute towed (NPUE).

Statistical analyses

Statistical analyses followed Sokal and Rohlf (1995). Parametric statistics were applied when the data conformed to the parametric assumptions of normality (Shapiro-Wilk test) and homogeneity of variances (Levene's test). Variables that did not conform to parametric assumptions were transformed to log (biomass or number)+1. Nonparametric statistics were employed only after appropriate methods were deemed unsuccessful in transforming the data to meet parametric assumptions. Both parametric and nonparametric statistical analyses were completed by using the STATISTICA software package (Statsoft Inc, 1999). Using *t*-tests, we evaluated the performance of the paired nets prior to the addition of the BRDs and compared the catchability of the BRD-equipped net to its control. Because we used a paired-tow design for field testing, we analyzed each net size and type of BRD separately; net sizes and BRDs were not directly compared with each other but were always compared with the controls. The ability of a BRD-equipped trawl to retain shrimp while reducing bycatch was assessed by comparing the CPUE (biomass) and NPUE of finfish and shrimp and by comparing the CPUE and the NPUE of the 10 most abundant finfish species in the BRD-equipped net with CPUE and NPUE data for its paired control net. The CPUE and NPUE of shrimp caught, calculated as described above, were based on actual weight and numbers of shrimp caught in each trawl. When the bycatch was subsampled, the finfish biomass or number was estimated using the formula

$$\textit{Finfish biomass or number} = \frac{\textit{Finfish subsample CPUE or NPUE} \times \textit{Total bycatch weight}}{\textit{Subsample weight}}.$$

Because our sampling period ranged over two seasons, we considered the interactive effects of season and net type (BRD-equipped or control) for each net size by using analysis of variance (ANOVA). We then used the least-squares difference (LSD) *post hoc* test to locate the significant differences. Differences between the net with the BRD and its paired control net in the size-frequency distribution of the 10 most abundant fish species were assessed by using the Kolmogorov-Smirnov two-sample test. To determine the percent reduction or increase in the biomass and number of each of the top ten finfish species, we compared the BRD-equipped nets with the control nets by using the untransformed mean CPUE and NPUE data for shrimp and finfish and the total number of individuals subsampled. Percent reduction for either CPUE or NPUE was then calculated (from Rogers et al., 1997) as

$$\textit{Percent difference} = \frac{(\textit{CPUE or NPUE of BRD net} - \textit{CPUE or NPUE of control net}) \times 100}{\textit{CPUE or NPUE of control net}}.$$

Results

No significant differences were found in total weight of the finfish or shrimp catch between nets of equal size prior to the addition of the BRDs. Similarly, the total weight of finfish or shrimp was not significantly affected by trawl position. The standardized mean ratio of finfish bycatch to shrimp biomass for all control net sizes combined was 5.3:1 (range 2.9:1–11.3:1). The standardized mean ratio for the BRD-equipped nets (3.8:1; range 2.5:1–4.9:1) was not significantly different but was substantially lower than that of the control nets.

CPUE and NPUE

In contrast to results with the control nets, there were no significant differences in either biomass or number of shrimp captured in the 17-m net or the 20-m net equipped with either BRD (Table 1). In winter, the biomass and the number of shrimp captured in the 14-m net equipped with either BRD were significantly lower than these quantities captured in the corresponding control net (FFE: P=0.025; EMF: P=0.008). On the contrary, both the biomass and number of finfish were significantly and notably lower in most of the BRD-equipped nets than they were in the control nets (for significant differences, P range for the FFE= 0.025–0.001 and P range for the EMF= 0.027–<0.001). The only exception was in the number of finfish caught in winter by nets equipped with either BRD.

Significant seasonal differences always occurred in shrimp CPUE (FFE: P<0.001 for all tests; EMF P range: 0.003–<0.001) and nearly always occurred in shrimp NPUE (FFE P range: 0.003–<0.001; EMF P range: 0.002–0.001; exception: NPUE for the 17-m EMF-equipped net) and accounted for most of the variation in CPUE observed for each net size. Nearly all significant differences in shrimp CPUE and NPUE between seasons were due to a larger catch of shrimp in winter. The only significant interactive

Table 1

Comparison of percentage differences in shrimp and finfish biomass (CPUE) and number (NPUE) from the 14-m, 17-m, and 20-m nets equipped with the Florida fisheye (FFE) and extended mesh funnel (EMF) bycatch reduction devices (BRDs). CPUE is the mean weight (grams) caught per minute towed, and NPUE is the mean number of individuals caught per minute towed. Significance levels of < 0.05 are denoted by asterisks.

		Shrimp						Fish					
		CPUE			NPUE			CPUE			NPUE		
		BRD	control	% diff.	BRD	control	% diff.	BRD	control	% diff.	BRD	control	% diff.
FFE													
Fall 1996	14-m net	29	31	−6	2	2	−5	99	154	−35*	3	4	−34*
	17-m net	21	21	4	2	1	7	70	105	−33*	2	3	−41*
	20-m net	17	16	6	1	1	11	176	196	−11	3	5	−39
Winter 1997	14-m net	36	45	−20*	2	2	−16*	113	132	−14	4	4	3
	17-m net	55	59	−6	4	4	−5	119	124	−4	12	12	5
	20-m net	42	38	11	2	2	14	114	130	−12	7	6	28
EMF													
Fall 1996	14-m net	32	33	−5	2	2	−5	90	168	−46*	3	5	−39*
	17-m net	23	25	−9	2	2	−11	60	151	−60*	2	4	−60*
	20-m net	12	12	0	1	1	0	116	174	−33*	3	5	−28*
Winter 1997	14-m net	42	60	−29*	2	3	−25*	106	130	−18	7	6	28
	17-m net	31	39	−18	2	2	−21	86	121	−28*	8	7	7
	20-m net	25	22	18	1	1	17	133	169	−21	5	4	12

effect between season and BRD type occurred in shrimp CPUE for the 14-m, EMF-equipped net (P=0.027).

Similarly, finfish CPUE differed seasonally for most net sizes (FFE P range: 0.009–< 0.001; EMF P for all tests: <0.001; exceptions: 14-m and 17-m, EMF-equipped nets), and NPUE differed seasonally for all net sizes (FFE P for all tests: <0.001; EMF P range: <0.001–0.000). However, the season in which the largest catch was harvested differed between net sizes and between BRD types. Both finfish CPUE and NPUE were significantly higher during winter than during fall in the 14-m and 17-m FFE-equipped nets but finfish CPUE and NPUE were significantly lower during fall than during winter in the 20-m FFE-equipped net. For the EMF-equipped nets, finfish CPUE differed seasonally only in the 20-m nets; CPUE in winter was higher than in fall. Finfish NPUE values for the EMF-equipped nets were always significantly higher in winter (P for all tests: <0.001).

Percent reduction

Differences in the percentage of shrimp in the BRD-equipped versus the control nets varied with season, net size, and BRD type. Although many of these differences were not significant (Table 1), patterns in shrimp loss or retention were apparent. Other than the 17-m, FFE-equipped net in fall, the addition of a BRD to a 14-m or 17-m net resulted in a reduction in shrimp CPUE and NPUE, regardless of BRD type. However, the reductions were significant only for the 14-m nets in winter. In contrast, shrimp CPUE and NPUE usually were slightly higher in the 20-m BRD-equipped nets than in the control nets.

Finfish CPUE was always less in BRD-equipped nets than in control nets (Table 1). The reduction in finfish bycatch CPUE was nearly always significant in fall, and most reductions were dramatic (20–60%). Reductions in finfish NPUE also had a strong seasonal component. For all net sizes, finfish bycatch NPUE in the BRD-equipped nets was notably (and nearly always significantly) less than that in the control nets in fall, whereas more (but not significantly more) finfish were captured in the BRD-equipped nets than in the control nets in winter.

Catch composition

Most of the biomass in both the BRD-equipped and the control nets usually was composed of finfish (30–70%). The remainder of the catch consisted of shrimp (15–20%), horseshoe crabs (*Limulus polyphemus*) and blue crabs (*Callinectes sapidus*) (15–58%), and miscellaneous invertebrates such as ctenophores, portunid crabs, sponges, and gastropods (<25%). When the catch of arthropods (principally horseshoe crabs) was large, the finfish catch was generally small. The shrimp catch was relatively stable even when the bycatch composition fluctuated.

Horseshoe crabs were the most abundant invertebrate bycatch species. A total of 2867 horseshoe crabs were caught during the two sampling seasons; largest catches occurred during fall. Although the catch of horseshoe crabs caught in the BRD-equipped nets was generally smaller

than the catch in the corresponding control nets, only in the 14-m FFE-equipped net and the 20-m EMF-equipped net was the number of horseshoe crabs caught significantly lower than the number of horseshoe crabs caught in the corresponding control nets (P=0.001 and P=0.05, respectively). Blue crabs were the second most abundant invertebrate bycatch species. A total of 544 blue crabs were caught during the two sampling seasons; the largest catches occurred during winter. Although fewer blue crabs were caught in the BRD-equipped nets, only in the 14-m EMF-equipped net was the number of blue crabs significantly lower than that in the corresponding control net (P=0.005 for both seasons).

A total of 44 species of finfish were caught during our study (Table 2). Numerically, ten finfish species composed more than 92% of the total finfish count, and a single species, the leopard searobin (*Prionotus scitulus*), composed over 40%. Abundance differed greatly between seasons for nearly all fishes (Table 2). The silver jenny (*Eucinostomus gula*), hardhead catfish (*Arius felis*), gafftopsail catfish (*Bagre marinus*), sand seatrout (*Cynoscion arenarius*), and silver perch (*Bairdiella chrysoura*) predominated in the catch during fall. These were replaced during winter by the leopard searobin (*Prionotus scitulus*), blackcheek tonguefish (*Symphurus plagiusa*), southern kingfish (*Menticirrhus americanus*), pinfish (*Lagodon rhomboides*), and spadefish (*Chaetodipterus faber*).

Ten of the finfish species that we captured are important to the recreational or commercial fishing sectors. These are the southern kingfish (*Menticirrhus americanus*), scaled sardine (*Harengula jaguana*), striped anchovy (*Anchoa hepsetus*), bay anchovy (*Anchoa mitchelli*), spot (*Leiostomus xanthurus*), spotted seatrout (*Cynoscion nebulosus*), gulf menhaden (*Brevoortia patronus*), gulf flounder (*Paralichthys albigutta*), pompano (*Trachinotus carolinus*), and permit (*Trachinotus falcatus*). These species each accounted for less than 1% of the total finfish count, except for the southern kingfish, which accounted for 4.6%.

For the species captured principally in fall, the overall proportion of the bycatch excluded by the 14-m and 17-m BRD-equipped nets was similar, and both sizes of nets tended to exclude high percentages of these fishes (Fig. 4). The 20-m BRD-equipped net was not as effective in reducing the numbers of these species. For the species captured principally in winter, the efficiency with which the BRD-equipped nets excluded these fishes varied among net sizes and BRD types. For some species (e.g. the leopard searobin and blackcheek tonguefish), BRD-equipped nets retained more individuals than did the corresponding control nets.

Size distribution

Shrimp size-frequency distributions for pooled trawls (BRD-equipped net and its corresponding control) had significant seasonal variation (P<0.001, t=16.1, df=2,416). In fall, mean carapace length was 23.4 mm (SD=4.7 mm) and the range was 11.2–40.4 mm, whereas in winter, the mean was 27.0 mm (SD=6.5 mm) and the range was 7.3–43.8 mm.

Mean sizes of the 10 most abundant finfish species differed significantly between the BRD-equipped nets and their corresponding controls in approximately 25% of the trawls with the FFE-equipped nets and in 30% of the trawls with the EMF-equipped nets (Table 3). The differences in mean sizes of individuals were usually small regardless of statistical significance. Nevertheless, the ratio of comparisons in which mean size of fish from BRD-equipped nets was smaller than that of fish from control nets to comparisons in which the mean size of fish from BRD-equipped nets was larger than that of fish from control nets was 2:1 for the trawls with the FFE-equipped net and 3:1 for the trawls with the EMF-equipped net. The only net size and BRD-type combination for which the mean size of individuals from the BRD-equipped net was always smaller than that from the control net was the 14-m FFE-equipped net.

Discussion

Shrimp catch

Although most BRD-equipped nets retained less biomass and fewer numbers of shrimp than did their corresponding control nets, the difference in these measures between the BRD-equipped nets and their controls was significant only for the 14-m net in winter. Indeed, shrimp biomass and number in the 20-m BRD-equipped net slightly exceeded biomass and number in the corresponding control net. In previous studies, researchers evaluating the efficiency of BRDs also found that the shrimp catch in BRD-equipped nets tended to be higher than in control nets. They attributed the increase in shrimp catch in their BRD-equipped net to a greater net spread caused by a reduction in the amounts of bycatch and drag (Rogers et al., 1997; Coleman and Koenig[10]) and to an increase in the volume of water filtered through the net due to the position of the BRD (Christian et al.[13]).

The numbers of shrimp retained in all BRD-equipped nets and in nearly all control nets were greater in winter than in fall. In the Tampa Bay region, adult female shrimp migrate out of the bay to spawn during spring and fall and juvenile shrimp are recruited into the bay during summer and winter (Eldred et al., 1965). The increase in abundance and the larger size range of shrimp that we caught during winter support this finding.

Finfish bycatch

Overall, both BRDs proved to be highly effective in reducing finfish bycatch without greatly reducing shrimp catch. The reduction in bycatch was usually significant in the 14-m and 17-m BRD-equipped nets. The mean ratio of finfish biomass to shrimp biomass in our BRD-equipped nets was within the range of ratios reported by others who tested the BRD-equipped nets in the Gulf (Alverson et al., 1994; GSAFDF[2]). Branstetter (1997) and Watson et al.[15]

[15] Watson, J., A. Shah, and D. Foster. 1997. Report on the status of bycatch reduction device (BRD) development. National Marine Fisheries Service, Mississippi Laboratories, P.O. Drawer 1207, Pascagoula, MS, 39568.

Table 2

Percentage contribution of individual finfish species subsampled from catches of otter trawls towed in Tampa Bay during fall 1996 and winter 1997. All tows have been pooled and incorporate both BRD-equipped and control nets for all three trawl-net sizes. Seasonal percentages are calculated for each species.

Common name	Species	Total number of sampled fish	% (Total)	% (Fall)	% (Winter)
Leopard searobin	*Prionotus scitulus*	28,299	41.02	6.6	93.4
Silver jenny	*Eucinostomus gula*	9134	13.24	86.2	13.8
Gafftopsail catfish	*Bagre marinus*	6658	9.65	83.5	16.5
Blackcheek tonguefish	*Symphurus plagiusa*	4613	6.69	35.6	64.4
Sand seatrout	*Cynoscion arenarius*	3365	4.88	80.6	19.4
Southern kingfish	*Menticirrhus americanus*	3193	4.63	44.0	56.0
Hardhead catfish	*Arius felis*	2949	4.27	88.0	12.0
Silver perch	*Bairdiella chrysoura*	2463	3.57	64.1	35.9
Pinfish	*Lagodon rhomboides*	1503	2.18	0.8	99.2
Spadefish	*Chaetodipterus faber*	1487	2.16	10.7	89.3
Bighead searobin	*Prionotus tribulus*	759	1.10	12.9	87.1
Scaled sardine	*Harengula jaguana*	642	0.93	59.4	40.6
Hogchocker	*Trinectes maculatus*	538	0.78	37.7	62.3
Striped anchovy	*Anchoa hepsetus*	524	0.76	25.5	74.5
Southern puffer	*Sphoeroides nephelus*	346	0.50	5.2	94.8
Southern hake	*Urophycis floridana*	337	0.49	0.0	100.0
Bay anchovy	*Anchoa mitchelli*	320	0.46	1.3	88.7
Pigfish	*Orthopristis chrysoptera*	274	0.40	3.7	96.3
Inshore lizardfish	*Synodus foetens*	237	0.34	76.4	23.6
Lined sole	*Achirus lineatus*	160	0.23	26.8	73.2
Lookdown	*Selene vomer*	138	0.20	100.0	0.0
Atlantic bumper	*Chloroscombrus chysurus*	135	0.20	97.7	2.3
Striped burrfish	*Chilomycterus schoepfi*	128	0.19	2.3	97.7
Ocellated flounder	*Ancylopsetta quadrocellata*	93	0.13	1.1	98.9
Spot	*Leiostomus xanthurus*	89	0.13	0.0	100.0
Crested blenny	*Hypleurochilus geminatus*	82	0.12	1.2	98.8
Rough silverside	*Membras martinica*	78	0.11	24.4	75.6
Planehead filefish	*Monacanthus hispidus*	76	0.11	15.7	84.3
Threadfin herring	*Opisthonema oglinum*	72	0.10	38.8	61.2
Scrawled cowfish	*Lactophrys quadricornis*	64	0.09	3.2	96.8
Crevalle jack	*Caranx hippos*	47	0.07	100.0	0.0
Sheepshead	*Archosargus probatocephalus*	46	0.07	97.8	2.2
Spotted seatrout	*Cynoscion nebulosus*	43	0.06	100.0	0.0
Orange filefish	*Aluterus schoepfi*	22	0.03	9.1	90.9
Gulf menhaden	*Brevoortia patronus*	19	0.03	68.4	31.6
Gulf toadfish	*Opsanus beta*	15	0.02	13.4	86.6
Harvestfish	*Peprilus alepidotus*	10	0.01	50.0	50.0
Leatherjacket	*Oligoplites saurus*	6	0.01	100.0	0.0
Shrimp eel	*Ophichthus gomesi*	5	0.01	80.0	20.0
Gulf flounder	*Paralichthys albigutta*	5	0.01	40.0	60.0
Gulf butterfish	*Peprilus burti*	4	0.01	50.0	50.0
Striped mojarra	*Diapterus plumieri*	1	0.00	100.0	0.0
Pompano	*Trachinotus carolinus*	1	0.00	100.0	0.0
Permit	*Trachinotus falcatus*	1	0.00	100.0	0.0

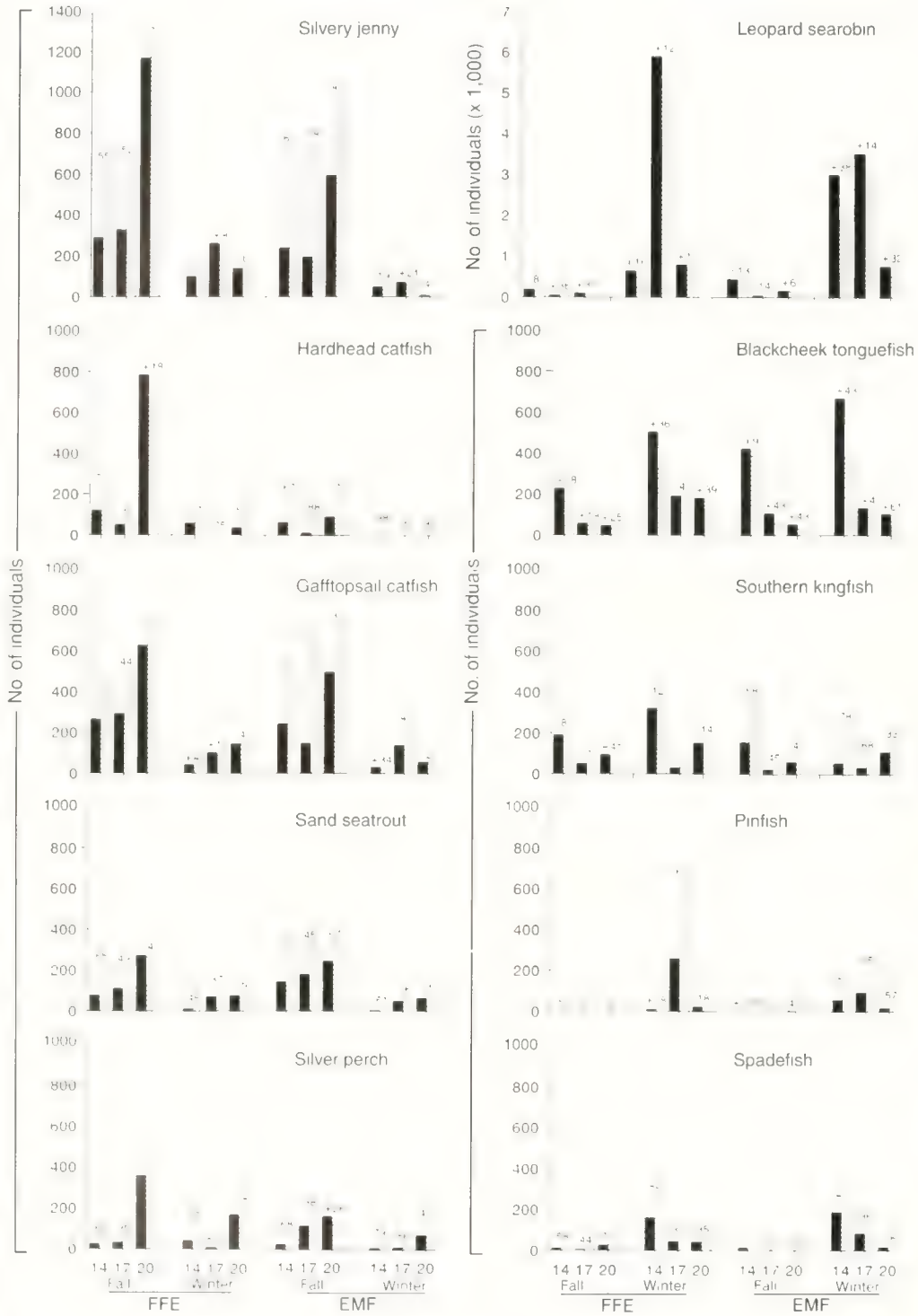

Figure 4

Comparisons of species-specific seasonal catch and retention rates for the 10 finfish species most commonly captured in the three sizes of period bycatch reduction device (BRD)-equipped nets (black bars) and control shrimp-trawl nets (hatched bars). Each vertical bar represents the total number of fish captured in 20 tows. Numbers over pairs of bars are the percent losses or gains in numbers of individuals captured by the BRD-equipped net versus the paired control net. FFE = Florida fisheye BRD; EMF = extended mesh funnel BRD. Column 1 shows species captured principally in fall; column 2 shows species captured principally in winter.

Table 3

Comparison of mean standard length measurements (mm) of the most abundant species caught in nets equipped with either the Florida fisheye (FFE) or the extended mesh funnel (EMF) bycatch reduction device (BRD) and their corresponding control nets. The three nets of different sizes used are denoted by the measurements of their perimeters: 14 m, 17 m, and 20 m. Significance levels are ≤0.05(*). Values represent mean and standard deviation, and sample sizes (n) are shown in parentheses. Dashes indicate that no fish were captured.

		Fall			Winter		
		14 m	17 m	20 m	14 m	17 m	20 m
Common name	Treatment	Mean, SD (n)	Mean, SD (n)	Mean, SD (n)	Mean, SD (n)	Mean, SD (n)	Mean, SD (n)
Florida fisheye bycatch reduction device							
Leopard searobin	BRD	103, 26 (191)	83, 13 (47)	98, 22 (85)	94*, 22 (327)	78, 17 (400)	97, 17 (309)
	Control	108, 24 (204)	90, 26 (30)	100, 22 (63)	96, 19 (317)	77, 13 (400)	97, 16 (325)
Silver jenny	BRD	66*, 09 (259)	75, 14 (286)	76, 08 (340)	82*, 07 (99)	73, 09 (180)	86, 07 (123)
	Control	69, 09 (394)	75, 10 (371)	76, 08 (339)	84, 09 (113)	82, 09 (189)	88, 12 (136)
Gafftopsail catfish	BRD	123*, 10 (203)	134, 13 (267)	124*, 10 (317)	143, 30 (43)	154, 26 (103)	147, 19 (131)
	Control	132, 10 (302)	131, 08 (347)	123, 16 (326)	136, 11 (26)	152, 23 (88)	147, 17 (140)
Blackcheek tonguefish	BRD	115*, 16 (214)	123, 20 (58)	121, 20 (48)	117, 15 (374)	155, 16 (185)	115*, 16 (160)
	Control	119, 16 (154)	125, 18 (47)	122, 19 (36)	120, 18 (293)	115, 18 (180)	119, 16 (111)
Sand seatrout	BRD	135*, 29 (78)	150*, 30 (110)	150, 33 (226)	177, 30 (12)	167, 29 (71)	174*, 22 (71)
	Control	146, 29 (217)	157, 26 (213)	155, 30 (225)	159, 27 (23)	169, 18 (71)	181, 30 (88)
Southern kingfish	BRD	137, 34 (185)	158, 14 (50)	135, 33 (93)	154*, 22 (275)	149, 33 (31)	170*, 21 (146)
	Control	138, 34 (202)	143, 35 (54)	136, 34 (55)	153, 24 (311)	142, 33 (35)	164, 20 (171)
Hardhead catfish	BRD	94*, 30 (120)	109, 48 (54)	94, 29 (325)	196, 88 (58)	180, 127 (2)	158, 79 (34)
	Control	101, 37 (224)	99, 32 (80)	99, 41 (304)	206, 80 (79)	199, 66 (8)	173, 73 (83)
Silver perch	BRD	88, 16 (23)	84, 17 (33)	89, 15 (224)	114, 11 (42)	94, 05 (10)	108, 07 (162)
	Control	90, 10 (58)	92, 17 (61)	89, 14 (235)	110, 11 (131)	97, 15 (9)	109, 11 (224)
Pinfish	BRD	90 (1)	—	86, 23 (2)	93, 17 (11)	79, 07 (159)	84, 14 (23)
	Control	103, < 1 (2)	–	97, 23 (2)	96, 11 (9)	78, 06 (194)	84, 13 (27)

continued

investigated the effectiveness of BRD designs that were similar to ours in offshore waters of the Gulf and the south Atlantic. They reported reductions in finfish biomass of 4–46% for the FFE and 18–35% for the EMF and respective reductions in shrimp biomass of 0–16% and 0–4%.

Our biomass reduction ratios of finfish to shrimp ranged broadly and unpredictably among net sizes and between BRD types and seasons, and our percentages of change in both biomass and numbers of finfish ranged widely between the BRD-equipped nets and their corresponding controls. In our study, the proportion of finfish to invertebrates and the species compositions and size distributions of these two groups influenced the ratio of finfish to shrimp. Bycatch reduction and shrimp retention have also

Table 3 (continued)

		Fall			Winter		
		14 m	17 m	20 m	14 m	17 m	20 m
Common name	Treatment	Mean, SD (*n*)	Mean, SD (*n*)	Mean, SD (*n*)	Mean, SD (*n*)	Mean, SD (*n*)	Mean, SD (*n*)
Extended mesh funnel bycatch reduction device							
Leopard searobin	BRD	104, 23 (317)	80, 26 (43)	99, 21 (110)	91, 22 (391)	86, 20 (359)	101, 14 (155)
	Control	108, 19 (310)	92, 26 (50)	95, 22 (121)	91, 21 (383)	85, 19 (359)	100, 15 (152)
Silver jenny	BRD	67‡, 09 (217)	76*, 09 (187)	74, 09 (360)	81, 07 (51)	76*, 07 (70)	87, 08 (10)
	Control	70, 09 (379)	78, 09 (381)	74, 08 (375)	80, 09 (62)	82, 12 (58)	95, 12 (19)
Gafftopsail catfish	BRD	129*, 12 (167)	132*, 12 (119)	125*, 18 (309)	147, 28 (32)	139*, 19 (139)	149, 19 (57)
	Control	124, 09 (343)	129, 19 (385)	121, 10 (394)	137, 15 (21)	148, 33 (185)	154, 17 (58)
Blackcheek tonguefish	BRD	115*, 15 (315)	126, 19 (107)	124, 18 (45)	122, 18 (346)	111, 20 (134)	114, 17 (99)
	Control	118, 16 (318)	129, 23 (61)	124, 17 (31)	122, 18 (273)	117, 19 (127)	117, 15 (41)
Sand seatrout	BRD	141*, 24 (144)	142, 29 (179)	145, 31 (227)	163, 37 (5)	159, 34 (51)	154*, 50 (57)
	Control	149, 32 (274)	146, 31 (289)	147, 28 (328)	144, 52 (13)	169, 22 (69)	179, 29 (60)
Southern kingfish	BRD	139, 28 (154)	127, 43 (22)	143, 27 (60)	153, 23 (54)	155, 29 (33)	167, 17 (85)
	Control	139, 25 (311)	138, 34 (40)	141, 29 (99)	155, 26 (210)	157, 26 (103)	173, 16 (120)
Hardhead catfish	BRD	100‡, 25 (65)	103, 44 (12)	100*, 38 (86)	94 (1)	301, 52 (2)	150, 50 (2)
	Control	95, 27 (193)	100, 38 (98)	103, 50 (167)	242, 72 (41)	227, 74 (22)	234, 54 (21)
Silver perch	BRD	91, 10 (25)	82*, 14 (116)	87, 12 (106)	104,‡ 12 (9)	98, 08 (12)	113, 10 (73)
	Control	93, 11 (78)	87, 14 (189)	82, 14 (121)	112, 09 (42)	103, 23 (27)	111, 10 (126)
Pinfish	BRD	84 (1)		130, 35 (4)	79, 05 (49)	76‡, 06 (81)	82, 09 (16)
	Control			—	79, 06 (108)	79, 07 (102)	81, 08 (38)

varied greatly in other studies. This variation has been attributed to temporal and spatial diversity in size and species composition of the finfish and shrimp within a trawling area; changes in bottom substrate; water depth; BRD type, placement, and size; trawl dynamics; and speed, and duration of tow (Branstetter, 1997; Fuls and McEachron[16]).

Although most of the nets tested in these other studies were considerably larger than the nets tested in our study, some of these attributes probably contributed to the variation that we observed. In addition, and most notably, the efficiency of our BRDs was greatly reduced when large numbers of horseshoe crabs were captured or when large numbers of spiny fishes became entangled in the nets.

Although the number and weight of finfish captured were greatly reduced in the FFE-equipped nets, finfish bycatch reduction rates were even higher with the nets equipped with the EMF, particularly the 17-m net, which had the highest overall reduction rate of all BRD and net-

[16] Fuls, B. E., and L. W. McEachron. 1998. Evaluation of bycatch reduction devices in Aransas Bay during the 1997 spring and fall commercial bay-shrimp season. Corpus Christi Bay National Estuary Program Publication CCBNEP-33, 6300 Ocean Drive, Corpus Christi, TX 78412, 33 p.

size combinations. Similar, comparatively high reduction rates for nets equipped with an EMF have been reported elsewhere (Fuls and McEachron[16]).

Both BRDs reduced (usually notably and significantly) the biomass of finfish in all net sizes during both seasons. However, the number of fish in the BRD-equipped nets compared with the control nets varied markedly between seasons. In fall, the number of fish in the BRD-equipped nets was nearly always much lower than the number in the corresponding control nets; but in winter, the number in the BRD-equipped nets was generally slightly higher than the number in the corresponding control nets. This increase was due to the sizable influx of juvenile leopard searobins in the finfish catch in winter. The long pectoral-fin rays on these fish became entangled in the nets (and in the BRD) and prevented the fish from escaping.

The detailed analysis of species-specific change in numbers of fish in the BRD-equipped nets compared with their corresponding control nets revealed additional interesting patterns. The number of silver jennys was reduced in all BRD-equipped nets, except in the 17-m BRD-equipped net during winter. The numbers of hardhead catfish, sand seatrout, silver perch, and southern kingfish were always reduced in the BRD-equipped nets except in the 20-m FFE-equipped net during fall. The number of leopard searobins and blackcheek tonguefish nearly always increased in the BRD-equipped nets, regardless of season. With some exceptions, larger fish were more likely to escape than smaller fish, probably because swimming ability is positively associated with size in fishes (Wardle, 1993). However, fish (particularly large individuals) of species with protruding bony scutes or long fin rays (e.g. gafftopsail catfish, leopard searobin, southern kingfish) became entangled in the nets and thus could not escape. The potential for large individuals of these types of fish to become entangled in the net may have increased because of the restricted net circumference, caused by the presence of the EMF. Thus, for these types of species, mean size of individuals retained in the BRD-equipped nets was frequently larger than mean size of individuals retained in the corresponding control nets.

A number of factors other than morphological features, such as pointed, projecting body structures, influence the ability of fish to escape from trawl nets equipped with BRDs. The behavior of fish in response to trawls has been described as a combination of optomotor response and rheotactic reaction, both of which contribute to a fishes' ability to escape capture in a trawl (Watson[17]). When ambient light conditions and water clarity allow for sufficient contrast between the trawl and the background, many, but not all, fishes orient their heads toward the mouth of trawl and maintain swimming speeds comparable to the trawling speed. Thereby, a fish can align itself with the in-trawl current. This optomotor response is usually associated with the well-developed lateral line system found in pelagic schooling species and is usually absent in demersal species (Pavlov, 1969). However, this response is considerably diminished during nighttime and in turbid water, and both of these conditions existed during our trawling. Thus, fishes with well-developed optomotor responses probably required additional stimuli to escape from our nets, even if they were in close proximity to an escape opening. Most of these fishes may have escaped the trawl through the BRD when the trawl speed was reduced during trawl haul-back (Watson[17]). The rheotactic response allows demersal fish to detect turbulent water flows and associated pressure gradients through the lateral line even when substantial visual cues are not available (Wardle, 1993). Areas of disturbed water exist within a moving trawl, especially near objects such as BRDs, which interrupt water flow. Demersal fishes with well-developed rheotactic responses can sense these areas of reduced velocity, align themselves behind these areas, and eventually escape through the exit provided by the BRD while the trawl is being towed. The finfish species with the largest percentage reductions in numbers in our BRD-equipped nets compared with the corresponding control nets were demersal and most likely used this response to assist in their escape.

BRDs and fishery management

Both the FFE and EMF are standard bycatch reduction devices recommended by NMFS and used by the shrimp industry. The effectiveness of these two BRDs in reducing finfish bycatch without greatly reducing shrimp catches has been well documented for the Gulf and the South Atlantic shrimp fisheries. (Captiva and Rivers, 1960; Gutherz and Pellegrin, 1988; Murray et al., 1992; Watson et al., 1993; Branstetter, 1997; Rogers et al., 1997; Coleman et al.[7]; Christian et al.[13]; McKenna and Monaghan[14]; Watson et al.[15]; our study). The FFE is now required in all shrimp trawls used in the federal Exclusive Economic Zone along the South Atlantic and in the Gulf.

The policy set forth by the FMFC in 1990 to reduce the overall finfish bycatch in the Florida shrimp fishery has been addressed in our study. In part as a result of this study, Florida is the first state bordering on the Gulf of Mexico to require the use of BRDs in state waters. BRDs not only serve to conserve natural marine resources, in the Florida shrimp fishery they provide additional benefits to the shrimp fishermen. Reducing bycatch decreases drag during tow times, which, in turn, lowers fuel consumption thereby reducing fuel costs, diminishes wear and tear on the trawl gear, decreases culling time by the deck crew, and produces a better shrimp product. From a cost-benefit perspective, BRDs clearly provide conservational, economic, and sociological benefits that far outweigh their actual costs.

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[17] Watson, J. W. 1988. Fish behavior and trawl design: potential for selective trawl development. *In* Proceedings of the world symposium on fishing gear and fishing vessel design, (S. G. Fox and J. Huntington, eds.), p. 25–29. Newfoundland and Labrador Institute of Fisheries and Marine Technology, P.O. Box 4920, St. John's, Newfoundland A1C 5R3.

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Severe decline in abundance of the red porgy (*Pagrus pagrus*) population off the southeastern United States

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Abstract—Status of the southeastern U.S. stock of red porgy (*Pagrus pagrus*) was estimated from fishery-dependent and fishery-independent data, 1972–97. Annual population numbers and fishing mortality rates at age were estimated from virtual population analysis (VPA) calibrated with fishery-independent data. For the VPA, a primary matrix of catch at age was based on age-length keys from fishery-independent samples; an alternate matrix was based on fishery-dependent keys. Additional estimates of stock status were obtained from a surplus-production model, also calibrated with fishery-independent indices of abundance.

Results describe a dramatic increase in exploitation of this stock and concomitant decline in abundance. Estimated fully recruited fishing mortality rate (F) from the primary catch matrix increased from 0.10/yr in 1975 to 0.88/yr in 1997, and estimated static spawning potential ratio (SPR) declined from about 67% to about 18%. Estimated recruitment to age 1 declined from a peak of 3.0 million fish in 1973–74 to 94,000 fish in 1997, a decline of 96.9%. Estimated spawning-stock biomass declined from a peak of 3530 t in 1979 to 397 t in 1997, a decline of 88.8%. Results from the alternate catch matrix were similar. Retrospective patterns in the VPA suggest that the future estimates of this population decline will be severe, but may be less than present estimates.

Long-term and marked declines in recruitment, spawning stock, and catch per unit of effort (both fishery-derived and fishery-independent) are consistent with severe overexploitation during a period of reduced recruitment. Although F prior to 1995 has generally been estimated at or below the current management criterion for overfishing (F equivalent to SPR=35%), the recent spawning-stock biomass is well below the biomass that could support maximum sustainable yield. Significant reductions in fishing mortality will be needed for rebuilding the southeastern U.S. stock.

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Fish. Bull. 100:351–375 (2002).

New analyses of the red porgy (*Pagrus pagrus*) stock off the southeastern U.S. coast indicate that dramatic changes in age structure and population abundance have occurred over the last 25 years. The red porgy, a protogynous sparid also known as silver snapper and pink snapper, associates with reefs and is commonly found over irregular and low-profile hard bottoms at depths between about 20 and 200 m (Manooch and Hassler, 1978). The species has been an important component of the snapper-grouper complex in the coastal Atlantic Ocean off the southeastern United States, particularly off North and South Carolina.

This study is the first complete assessment of red porgy in this region since 1986 (Vaughan et al., 1992). We introduce methodological improvements that strengthen analyses considerably, including fishery-independent data to calibrate the virtual population analysis (VPA), as recommended in a recent review of marine stock assessments (NRC, 1998). Extensive analyses were made of the sensitivity of major results (estimates of abundance and fishing mortality rate) to assumptions. Sensitivity analyses (in the broad sense) included separate VPAs on two catch matrices, one based on fishery-independent age-length keys and the second on fishery-derived keys; estimation with different assumptions about natural mortality rate; a retrospective analysis; alternate treatments of zeroes in an abundance index; and the use of a surplus-production model to provide complementary estimates of stock abundance and management benchmarks. Robustness of major conclusions to these factors and relatively close agreement between estimates from catch-at-age models and production models strengthen the finding that the red porgy stock was severely depleted at the close of 1997.

Range, stock structure, and reproductive biology

Red porgy have an extensive range—they are found off the southeastern U.S. Atlantic coast; in the Gulf of Mexico; off the South American Atlantic coast from Brazil to Argentina; off Portugal and Spain; in the Mediterranean Sea; off west Africa south to the Cape Verde Islands; and around the Azores, Madeira, and Canary Islands. The stock unit analyzed in our study includes fish from U.S. Atlantic waters off North Carolina (NC) south of Cape Hatteras; South Carolina (SC); Georgia (GA); and the east coast of Florida (FL). This range expands that previously defined for the stock, which (Vaughan et al., 1992; Huntsman et al.[1]) included fish only from waters off NC and SC. Within the current stock definition, red porgy have been most abundant from NC and SC waters. Tagging studies

[1] Huntsman, G. R., D. S. Vaughan, and J. C. Potts. 1993. Trends in population status of the red porgy *Pagrus pagrus* in the Atlantic Ocean of North Carolina and South Carolina, USA, 1971–1992. South Atlantic Fishery Management Council, 1 Southpark Circle, Charleston, SC 29407. [Available from Beaufort Laboratory, 101 Pivers Island Road, Beaufort, NC, 28516.]

have shown neither long-range migrations nor extensive local movements of adult red porgy (Manooch and Hassler, 1978), nor has circumstantial or anecdotal information suggested such movements. Peak spawning occurs from March through April (Manooch, 1976). Red porgy eggs and larvae are pelagic, hatch 28 to 38 h after fertilization, and can survive transport by ocean currents for 30 days or more (Manooch et al., 1981). Thus, the population off the U.S. Atlantic coast could in theory receive eggs or larvae from the Gulf of Mexico stock. However, because of the distances involved and the variability of ocean currents, the likelihood of significant population mixing in this way seems small, and we adopted the stock boundaries described above.

Red porgy attain maximum size slowly and live relatively long (an 18-year-old specimen is the oldest on record), but maturity occurs far younger. Roumillat and Waltz[2] collected red porgy between 1979 and 1987 along the continental shelf between Cape Fear, NC, and Cape Canaveral, FL, using trawl nets, traps, and hook-and-line gear. Life history information was obtained from 7104 red porgy; 5820 otoliths were examined (including 134 from historical or port samples), of which 5491 had discernable rings; estimation of sex composition was based on 6044 red porgy. Mature gonads were found in 18.8% of females at age 1, 85.2% at age 2, 99.7% at age 3, and 100% at older ages.

Red porgy are protogynous hermaphrodites. Thus, females predominate at smaller size intervals, but males occur in all age groups. Age-specific sex ratios reported by Roumillat and Waltz[2] (their Table 6) were used in our analyses: 89% female at age 1, 91% at age 2, 77% at age 3, 67% at age 4, 59% at age 5 , 51% at age 6, 25% at age 7, and 21% at age 8.

Methods

Fishery-dependent data sources and adjustments

In the study area (Cape Hatteras, NC, through the east coast of FL), three fisheries take red porgy: commercial, recreational, and headboat. Hook-and-line has been the most common commercial gear, but occasional significant landings are taken with trawls and traps. Trawling for red porgy has been banned since 1989 (Amendment 12 [SAFMC[3]]) The recreational fishery includes all recreational fishing from shore, from private boats and from charter boats (for-hire vessels that usually accommodate six or fewer anglers as a group). The headboat fishery (larger for-hire vessels that charge per angler) is sampled separately, and for that reason is distinguished here from other recreational fisheries. Recreational and headboat fisheries, like the commercial fishery, use hook-and-line gear almost exclusively. Data sources for all three fisheries are described in our study and summarized in Table 1.

Commercial fishery Landings statistics in weight for the commercial fishery, 1972–97, were obtained from the NMFS general canvass database (NMFS, Southeast Fisheries Science Center, Beaufort, NC, and Miami, FL). In addition, North Carolina commercial landing statistics by gear for red porgy were provided by NC Division of Marine Fisheries (NCDMF). Fishery-based length and weight statistics, 1983–97, were obtained from the NMFS Trip Interview Program (TIP) database. Length frequencies from SC commercial landings, 1976–80, were taken from Vaughan et al. (1992).

Commercial landings statistics, 1972–84, are recorded as "porgies," but include some other species. Following Vaughan et al. (1992), we multiplied such non-North-Carolina landings by 0.9 to approximate landings of red porgy only; North Carolina data were corrected by NCDMF before we received them. Commercial landings were available only in weight and were converted to counts by dividing catch in weight by mean weight per fish for the same gear and year. To compute annual mean weights, fish lengths from the TIP database were converted to weight with estimated weight–length relationships, described below.

Annual length-frequency distributions L were developed for commercial hook-and-line gear for each area (Carolinas vs. Florida), 1983–97. Commercial length frequencies for 1972–82 were taken from Vaughan et al. (1992). Because trap and trawl landings have been quite small since the mid–1980s and few fish have been sampled (1611 [trap]; 1455 [trawl], mostly between 1986 and 1988), two overall length-frequency distributions for each gear were used, one for 1972–89 and the other for 1990–97. Gear-specific commercial length-frequency distributions were weighted by catch in number by state to obtain catch at length by gear and state.

Recreational fishery Recreational catch and effort estimates and data on length and weight composition, 1979–97, were obtained from the NMFS Marine Recreational Fisheries Statistics Survey (MRFSS) database (Gray et al., 1994; Marine Recreational Fisheries Statistics, 1999). Fishing modes used by MRFSS include shore-based, private-boat-based, and charter-boat based fishing. Within each mode, three catch types are defined: "A" catches were available to sampling personnel for identification and measurement; "B1" catches were unavailable because they had been used for bait, filleted, discarded dead, etc.; and "B2" catches were unavailable because they had been released. Postrelease mortality of B2 catches was assumed to be 18% (Dixon and Huntsman[4]). Following

[2] Roumillat, W. A., and C. W. Waltz. 1993. Biology of the red porgy *Pagrus pagrus* from the southeastern United States. Data report 1993 MARMAP, South Carolina Wildlife and Marine Resources Department, P.O. Box 12559, Charleston, SC 29422-2559.

[3] SAFMC (South Atlantic Fishery Management Council. 2000. Final, amendment number 12 to the fishery management plan for the snapper grouper fishery of the South Atlantic region. South Atlantic Fishery Management Council, Charleston, SC, 159 p. + appendices.

[4] Dixon, R. L. and G. R. Huntsman. 1993. Survival rates of released undersized fishes (abstract). Sixth Annual MARFIN Conference, Atlanta, GA, 12–13 October 1993. [Available from Beaufort Laboratory, 101 Pivers Island Road, Beaufort, NC, 28516.]

Table 1

Data sources for analysis of red porgy off the southeastern United States. Sample size n is number of fish lengths measured. Aging data sources are given in Table 2. Symbol N is number of fish, W, weight of fish caught.

Data source	Years	Database	Type	n
Commercial fishery	1972–97	NMFS, general canvass	Landings (W)	
	1972–97	NC Div. Mar. Fish.	NC landings (W)	—
	1983–97	NMFS trip interview	Lengths and weights	62,042
	1976–80	SCDNR (Vaughan et al., 1992)	Lengths	8855
Recreational fishery (private and charter boats)	1979–97	NMFS MRFSS	Catch (N and W)	—
			Lengths and weights	945
Headboat fishery	1972–97	NMFS headboat survey (NC, SC)	Catch (N and W)	—
			Lengths and weights	44,131
	1976–97	NMFS headboat survey (GA-N.E. FL)	Catch (N and W)	—
			Lengths and weights	1454
	1981–97	NMFS headboat survey (S.E. FL)	Catch (N and W)	—
			Lengths and weights	1166
Fishery-independent	1979–97	MARMAP hook and line	CPE (N) and lengths	2085
	1980–97	MARMAP traps (FL snapper and chevron)	CPE (N) and lengths	10,784

Vaughan et al. (1992), we adjusted the data to avoid duplication from inclusion of headboat landings in charter-boat landings reported by MRFSS, 1979–85.

Mean recreational landings by mode were calculated for 1979–97 and used for 1972–78, a period of minimal exploitation before MRFSS data were collected. Because recreational landings are a small fraction of the total, this procedure, while approximate, was better than assuming landings of zero in that period.

Recreational length-frequency distributions from MRFSS, 1979–97, were weighted by catch (A+B1) in number by mode, wave (2-month interval), and state. The minimal catch associated with shore-based fishing was pooled with the private-boat mode. Headboat length-frequency distributions from MRFSS (1979–85) were not used in development of catch matrices for the recreational fishery because more complete data were available from the headboat sampling program.

Headboat fishery Estimates of headboat catch in numbers and weight and fishing effort in angler-days (Table 1) were obtained from the NMFS (Beaufort, NC) headboat sampling program (Huntsman, 1976; Huntsman et al., 1978). Zero-intercept linear regression analyses on NC and SC data were used to estimate landings from GA to northeast FL and landings from southeast FL, and fishing effort back to 1972. Catch per effort (CPE) in numbers was calculated by dividing annual catch in numbers by annual effort.

Length samples from headboats were not available from GA or FL before 1976, nor from southeast FL before 1981. We used mean length-frequency distributions for 1976–80 to fill in for GA and FL, 1972–75, and length-frequency distributions from GA to northeast FL to fill in for southeast FL, 1976–80. Annual headboat length-frequency distributions from the headboat sampling program, 1972–97, were weighted by catch in numbers caught during that season (January–May, June–August, September–December), and geographic area (NC, SC, GA to northeast FL, southeast FL) to obtain catch in length by season and area.

Development of catch-at-age matrices

Estimates of catch at age in numbers were made by using an approach similar to that of Vaughan et al. (1992). Total catch in numbers (n, scalar) for each combination of time, gear, and area was multiplied by an age-length key (A, matrix of dimension $a \times b$); the product was multiplied by the corresponding length-frequency distribution (L, vector of length b) to obtain catch in numbers at age (N, vector of length a):

$$\mathbf{N} = n \cdot \mathbf{A} \cdot \mathbf{L}. \quad (1)$$

Here, a is the number of ages (for this study, ages 0 to 8^+) and b is the number of length intervals (for this study, 15 intervals of 25 mm each from 200 mm to 550^+ mm).

Age-length keys Separate age-length keys were developed from fishery-dependent and fishery-independent data. Fishery-dependent keys for 1972–74 were those of Manooch and Huntsman (1977); for 1986, those of Vaughan et al. (1992); for 1996–97, those of Potts and Manooch (2002). Keys for 1975–85 and 1987–95 were approximated by linear interpolation from available keys (method of Vaughan et al., 1992).

We constructed fishery-independent keys from samples taken in 1979–94 (Harris and McGovern, 1997) by the Marine Resources Monitoring, Assessment, and Prediction (MARMAP) Program, a fishery-independent sampling program of the SC Department of Natural Resources. In that study, 8660 red porgy were collected, primarily with hook and line and various traps, and preserved sagittae were used for age estimation. As a compromise between estimating annual keys based on smaller sample sizes and an overall key, which would disguise growth variability over time, we grouped MARMAP aging data into 3-yr periods, with the last four years divided instead into two 2-yr periods: 1979–81, 1982–84, 1985–87, 1988–90, 1991–92, 1993–94. Potts and Manooch (2002) aged 111 red porgy collected during 1996–97 by the MARMAP program (predominantly younger fish, maximum age of 6). We used an age-length key from those data for 1995–97. Where fewer than 10 fish occurred in a 25-mm total-length interval, we pooled the data over longer time periods.

No aging data are available from fishery-independent sources before 1979. We constructed a key, used for 1972–74, from fishery samples taken in those years (Manooch and Huntsman, 1977). For 1975–78, we interpolated linearly between that key and the earliest key derived from fishery-independent data (1979–81). Thus, the fishery-independent (primary) catch matrix described below reflects some fishery-dependent data in the earliest years.

Catch-at-age matrices Equation 1 was applied to each fishery-gear combination and catch-at-age estimates were accumulated for each year to obtain estimates of annual catch in numbers at age (the catch matrix), 1972–97. This was done twice, first by using the fishery-independent age-length keys to obtain the primary catch matrix, and then by using fishery-derived age-length keys to obtain the alternate catch matrix. (Although the designation of "primary" and "alternate" matrices is somewhat subjective, it was based on the more extensive and continuous quality of fishery-independent data, as discussed later. Despite the designation, most analyses were conducted twice, once with each matrix.) Final catch matrices each contained numbers of fish caught at ages 1 through 8+ in fishing years 1972 through 1997; partial recruitment for age-0 red porgy was essentially zero.

We judged coherence of catch matrices by examining pairwise correlations between ages as a cohort progressed through the fishery. For fully recruited ages and with F varying only moderately from year to year, we expected to be able to follow a strong or weak cohort through the catch matrices. Both matrices generally showed significant correlations ($P<0.1$) between lagged catches at adjacent ages. A few significant correlations were found among lagged catches for nonadjacent ages.

Growth in length and weight

Von Bertalanffy (1938) growth models were fitted from data on total length (mm) and age obtained from fishery-independent and fishery-dependent sources (Table 2). Disaggregated aging data could not be located for fishery-dependent data from 1972 to 1974 and from 1986; therefore observed midinterval lengths at age from keys were used for those years. For fishery-dependent data for 1989–98 and fishery-independent data for 1996–97, back-calculated length at oldest age was used, a procedure that avoids potential bias by the use of multiple measurements per fish (Vaughan and Burton, 1994). For fishery-independent data, 1979–94, observed length at age was used, adjusted for month of collection. The particularly high standard error associated with the estimate of L_∞ for fishery-independent data, 1996–97, was associated with a lack of fish older than 6 years of age in the sample (Table 2).

We estimated weight W (in kg) from total length L (in mm) by using the relationship $W = aL^b$. Parameter estimates were as follows: for fishery-dependent modeling, we used values from Manooch and Huntsman (1977) ($a = 2.524 \times 10^{-5}$ and b=2.894) for the 1970s and 1980s; and from Potts and Manooch (2002; a=8.85 $\times 10^{-6}$ and b=3.060) for the 1990s. For fishery-independent modeling, we used values for 1972–78 from Manooch and Huntsman (1977), and we estimated values for 1979–97 from MARMAP data, 1979–94, (a=3.064 $\times 10^{-5}$ and b=2.865).

Abundance indices

Fishery-independent data on length, weight, age, and CPE, 1979–97 (Table 1) were obtained through the MARMAP program (Collins and Sedberry, 1991; Harris and McGovern, 1997). In computing fishery-independent indices of abundance from those data, we used CPE from hook-and-line and trap gears only. We extended data from chevron trap, 1988–97, back to 1980 with data on Florida snapper trap, using a conversion factor determined by MARMAP (Collins, 1990; Vaughan et al., 1998); we refer to the resulting series as "extended" chevron trap. To obtain age-specific indices of abundance for hook-and-line, 1979–97, and extended chevron trap, 1980–97, we applied Equation 1, using CPE in place of n, and using annual MARMAP estimates of CPE, age-length keys, and length-frequency data for each gear.

Like the catch matrices, matrices of fishery-independent CPE estimates were examined for coherence through correlations among lagged CPE. The hook-and-line index showed greatest coherence among ages 1 through 4, whereas the extended chevron-trap index appeared quite coherent over a wider range of older ages (3 through 7).

Mortality estimation

Instantaneous total mortality rates (Z) were estimated from cohort-specific catch-curve analyses (Ricker, 1975) of the two catch matrices by using only ages that appeared fully recruited (4 through 7). Empirical approaches were also used to estimate total mortality rate (Z). The more complex of two methods presented by Hoenig (1983) is based on age of the oldest fish observed, sample size, and age of recruitment to the sampling procedure. Assuming those quantities to be 18 yr, 10,000 fish, and 1 yr, we estimated Z = 0.58/yr, a likely upper bound on M.

Table 2

Parameters of von Bertalanffy growth models for red porgy off southeastern United States. Maximum age in the sample is labeled t_{max}, sample size is n. Parameters estimated from observed mid-interval length at age in fishery-dependent data for 1972–74 and 1986; from back-calculated length at oldest age in fishery-dependent data for 1989–1998 and fishery-independent data for 1996–97; and from observed length at age adjusted for month of collection in fishery-independent data for 1979–94. Asymptotic standard error is in parentheses below corresponding parameter estimate.

Type of data and year	n	L_∞ (mm)	k	t_0	$t_{max(yr)}$	Range (mm)
Fishery-dependent data						
1972–74	1685	575.8 (2.5)	0.16 (0.002)	–1.88 (0.03)	15	185–640
1986	535	1252.9 (28.7)	0.40 (0.001)	–4.05 (0.04)	12	213–615
1989–98	492	796.6 (43.9)	0.09 (0.009)	–2.34 (0.23)	18	247–723
Fishery-independent (MARMAP) data						
1979–94	8601	485.5 (5.3)	0.23 (0.01)	–1.48 (0.06)	14	142–568
1979–81	1171	501.3 (5.4)	0.34 (0.01)	–0.15 (0.06)	13	142–557
1982–84	2159	626.1 (24.6)	0.15 (0.01)	–1.61 (0.14)	14	145–568
1985–87	2332	542.5 (20.4)	0.16 (0.01)	–2.24 (0.16)	12	176–523
1988–90	1268	424.2 (8.6)	0.31 (0.02)	–1.06 (0.14)	12	176–487
1991–92	842	425.1 (10.1)	0.25 (0.02)	–1.62 (0.20)	13	179–456
1993–94	829	375.7 (5.5)	0.43 (0.04)	–0.78 (0.18)	12	183–501
1996–97[1]	111	754.7 (246.3)	0.10 (0.05)	–1.27 (0.38)	6	151–384

[1] Otoliths from fish collected during 1996–97 by MARMAP but aged by C. Manooch and J. Potts (NOAA Beaufort Laboratory).

We estimated natural mortality rate empirically (Pauly, 1979) from parameters L_∞ and K of the von Bertalanffy growth function and mean environmental temperature. Estimates ranged from M = 0.27/yr to M = 0.57/yr, based on mean sea temperature of 22°C (Manooch et al., 1998) and the range of growth parameters estimated in our study (Table 2). A similar method, that of Ralston (1987) and based solely on growth parameter K, provided estimates from M = 0.22/yr to M = 0.64/yr. Given the uncertainty in M, we chose a base M = 0.28/yr (Vaughan et al., 1992). We also performed bracketing estimates of most quantities using M = 0.20/yr and M = 0.35/yr.

Fishing mortality rate F was estimated by subtracting the assumed natural mortality rate from the total mortality rate. These estimates of F were used only as terminal-year values in the separable VPA.

Virtual population analyses

Primary and alternate catch matrices were analyzed by using virtual population analysis (VPA) to obtain annual age-specific estimates of F and population size. First, a separable VPA (Doubleday, 1976; Pope and Shepherd, 1982), as implemented by Clay (1990), was used to estimate partial recruitment by age for later use in calibrated VPA. Data from 1992–97 were used for this purpose because a 12-inch minimum size limit was introduced in 1992 (amendment 4[SAFMC[5]]), and using data from both before and after imposition of the size regulation would likely violate the separability assumption. The starting value of F for the separable VPA was the mean of three final year-class estimates of Z (~0.78/yr), less M.; i.e. F ~ 0.50/yr.

A calibrated VPA (Pope and Shepherd, 1985; Gavaris, 1988) was then applied, as implemented in the FADAPT

[5] SAFMC (South Atlantic Fishery Management Council). 1991. Final, amendment 4, regulatory impact review, initial regulatory flexibility analysis and environmental assessment for the fishery management plan for the snapper grouper fishery of the South Atlantic region. South Atlantic Fishery Management Council, Charleston, SC, 99 p. + appendices.

computer program,[6] by using the two fishery-independent abundance indices (hook-and-line and extended chevron trap). Most calibrated VPA runs were made with both indices, but a few were made with individual indices to assess sensitivity. The hook-and-line index included estimates of zero in 1992 and 1996, to which a small value (0.0001) was added before log transformation, a technique often used in statistical ANOVA models (e.g. Snedecor and Cochran, 1980). Effects of that approach were explored by assuming missing values in place of zeroes in an additional calibrated VPA run.

Several additional techniques were used to examine sensitivity to assumptions. Sensitivity of estimated F and recruitment to age 1 to uncertainty in M was investigated by conducting the separable and calibrated VPAs with alternate values of M (0.20/yr and 0.35/yr). Retrospective analyses of the calibrated VPA were conducted to investigate the possibility of systematic deviations ("retrospective patterns") in estimates of F and recruitment in most recent years, in comparison to estimates obtained for the same years from later analyses. In the retrospective analyses, we varied the final year of data used from 1992 to 1997; the initial year was 1972 throughout.

For presentation of results, we averaged estimated quantities within three time periods: 1972–78, representing a lightly fished stock; 1982–86, representing the stock after increasing exploitation during the early 1980s; and 1992–96, representing conditions since the last major change in management (amendment 4[SAFMC[5]]), but omitting the terminal year (1997) to reduce retrospective effects (discussed below). We refer to these as early, middle, and recent periods. Recruitment was defined as the number of fish at age 1 on January 1.

Yield per recruit

Equilibrium yield per recruit (YPR) was estimated by the method of Ricker (1975), which divides the exploited life span into phases of constant mortality and growth rates; total YPR is obtained by summing yield across phases. Parameter estimates from YPR analysis were for both sexes and across the three time periods described above. It has long been recognized that fishing at F_{max} (F that maximizes YPR) can cause recruitment failure (Gulland and Boerema, 1973; Clarke, 1991; Caddy and Mahon, 1995), and the reference point $F_{0.1}$ was introduced as a more conservative alternative (Gulland and Boerema, 1973). Using most recent growth and selectivity, we computed both F_{max} and $F_{0.1}$.

Spawning potential ratio

Static spawning potential ratio (static SPR)—also known as equilibrium SPR or maximum spawning potential (Gabriel et al., 1989)—is a measure of fishing mortality rate scaled to a species' biology. Static SPR for a given fishing mortality rate F^* is computed as the ratio SPR = SS(F^*) / SS(0), where SS(F^*) is the spawning-stock size (lifetime cohort spawning contribution) expected under F^*, and SS(0) is the corresponding spawning-stock size expected under $F = 0$. Other life history parameters are assumed constant at most recent values. Increases in F reduce static SPR.

In species that do not change sex, spawning-stock biomass is usually computed as total mature female biomass or total egg production (Prager et al., 1987), quantities that are highly correlated. Because red porgy change sex, we used four representations of spawning-stock biomass: female mature biomass, male mature biomass, total (male + female) mature biomass, and total egg production, each assuming the sex ratios at age given above (Roumillat and Waltz[2]).

To compute total egg production, we used the relationship between fecundity (E, number of eggs) and total length (TL, mm) of Manooch (1976):

$$\ln E = -14.1325 + 4.3598\ (\ln TL), \qquad (2)$$

Sex ratio in the mature population can be changed by fishing. We estimated reduction in the proportion of males among mature fish from the proportion expected with no fishing and assuming that the rate of sex transformation is not affected by changes in population structure.

Spawner-recruit relationships

The relationship between spawning-stock biomass and resulting recruitment to age 1 was modeled by using the Beverton-Holt spawner–recruit function (Ricker, 1975):

$$R = \mathrm{SSB}/(b_0 \cdot \mathrm{SSB} + b_1), \qquad (3)$$

where R = recruitment;
SSB = spawning-stock biomass, and
b_0, b_1 = fitted parameters.

To reduce the influence of retrospective patterns, SSB and R series (estimated from VPA) used in recruitment modeling were terminated at 1992. We used total mature biomass, rather than the more usual female mature biomass, to represent SSB in recruitment modeling.

With the estimated stock-recruitment relationship, 500-year simulations of the stock were made to estimate equilibrium yield and spawning-stock biomass as functions of fishing mortality rate. The simulations used mean population numbers, 1992–96, as starting values. Age-specific selectivity for the same period and the most recent growth patterns were used throughout. We thus estimated MSY, B_{MSY}, and F_{MSY} for each catch matrix.

Surplus-production model

A surplus-production model was fitted to obtain additional estimates of management benchmarks and stock status. We used the Prager (1994, 1995) formulation and implementation of the continuous-time Graham-Schaefer (logis-

[6] FADAPT by V. R. Restrepo (International Commission for the Conservation of Atlantic Tunas, Calle Corazón de María, 8, Sixth Floor, 28002 Madrid, Spain).

tic) model (Schaefer, 1954, 1957; Pella, 1967; Schnute, 1977; Prager, 1994). The approach is an observation-error estimator assuming proportional error variance and conditioned on observed landings. We attempted to fit the generalized production model (Pella and Tomlinson, 1969; Fletcher, 1978) by similar methods. Data were total landings in weight, 1972–97, and CPE indices derived separately from fishery-independent hook-and-line and trap data, 1979–97.

Initial difficulty in obtaining estimates was traced to two years of zero CPE in the fishery-independent hook-and-line index. Because the fitting was conducted in logarithmic transform, zeroes could not be accommodated; our initial, unsuccessful approach was to substitute very small values. We obtained estimates through the alternate procedure of considering those values missing, which is statistically equivalent to setting the observation weights to zero.

Because some estimates were moderately sensitive to assumptions about the starting stock biomass, B_1, in relation to carrying capacity, K, we obtained estimates at a range of values, namely B_1/K = {0.55, 0.65, 0.75, 0.85, 0.95} , a range chosen to reflect the stock's lightly fished status before the first year (1972). Fixing the starting value of relative biomass can reduce variance of estimates considerably (Punt, 1990). Bootstrapping with 700 repetitions was used to estimate 80% bias-corrected confidence intervals (Efron and Tibshirani, 1986) on the central set of estimates (B_1/K=0.75).

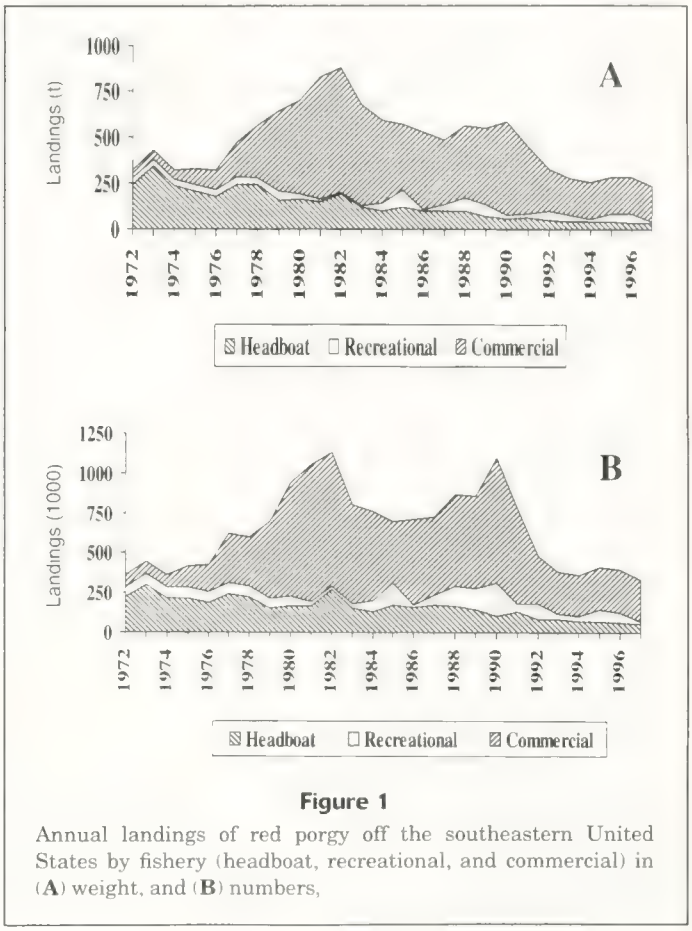

Figure 1

Annual landings of red porgy off the southeastern United States by fishery (headboat, recreational, and commercial) in (**A**) weight, and (**B**) numbers,

Results

In this section, all results are reported for the base value of M = 0.28/yr unless otherwise stated. Results reflect analysis of the primary catch matrix unless use of the alternate matrix is specifically mentioned.

Summary of landings and CPE

During the study period (1972–97), total landings in weight rose from about 325 t in 1972 to a maximum of 880 t in 1982 (Fig. 1A). Landings have been at or below 300 t since 1992, with 234 t in 1997. The headboat fishery accounted for about 52%–80% of total landings through 1977; commercial landings have been most prevalent since (Fig. 1B, Table 3). Maximum landings in numbers were about 1.13 million fish in 1982 (Table 4).

Commercial landings in weight rose from 45 t in 1972 to 678 t in 1982 and declined to 200 t/yr or less since 1992 (Fig. 1A); landings in numbers had a similar pattern (Fig. 1B). Commercial trawl landings averaged about 14% of commercial landings, 1972–84 but were quite small by 1985, and trawl gear was prohibited as of 12 January 1989 by amendment 1 to the Fishery Management Plan (amendment 12 [SAFMC[3]]). Hook-and-line landings have been about 95% of commercial landings by weight since 1985.

Recreational landings in numbers have shown no consistent trend, averaging about 70,000 fish per year, with some outstanding years of more than 100,000 fish between 1985 and 1990 (Fig. 1B). Catch by mode of fishing has been highly variable, but recreational landings have mainly been taken by charter boat (43% by number during the 1990s) and private boat (55%). Although remaining landings (<3%) are attributed to fishing for red porgy from shore, this amount is unlikely to be correct. These records may result from errors in recorded fishing mode or from erroneous species identification, but in either case would have negligible effect on our analyses.

Headboat landings have declined from 200,000 fish/yr during the 1970s to around 100,000–200,000 fish/yr in the 1980s and fewer than 100,000 fish/yr since (Fig. 1B). Most landings have come from NC and SC.

Mean weight in the commercial hook-and-line and headboat fisheries in the Carolinas has decreased, especially since about 1978 (Fig. 2). Mean weight in all fisheries combined has shown a general decline from 1972 to 1991 (Fig. 2) but has since increased somewhat.

All data on catch per effort (CPE) exhibited long-term decline. Declining headboat CPE was apparent from both NC and SC (Fig. 3). The fishery-independent abundance indices, also based on CPE, showed corresponding declines (Fig. 3): the extended chevron-trap index decline was precipitous; that in the hook-and-line index was similar, but somewhat less dramatic. (The CPE series derived from

Table 3

Red porgy landings in numbers (1000) by fishery, area, and gear or mode. Listed recreational landings from private boats include minor landings from shore.

	Commercial						Recreational and headboat							
	NC + SC			GA + FL			NC + SC			GA + FL				
Year	Trawl	Traps	Lines	Trawl	Traps	Lines	Private	Charter	Headboat	Private	Charter	Headboat	Commercial	Recreational and headboat
1972	0.6	22.9	0.9	0.2	1.3	45.4	31.7	27.1	201.4	9.9	1.0	18.6	71.1	289.7
1973	13.5	9.8	2.1	0.0	0.2	50.9	31.7	27.1	274.4	9.9	1.0	25.3	76.4	369.4
1974	0.0	20.3	3.5	0.0	0.5	47.5	31.7	27.1	201.3	9.9	1.0	18.6	71.8	289.5
1975	1.2	31.5	3.0	0.0	0.5	95.7	31.7	27.1	197.3	9.9	1.0	18.2	131.9	285.2
1976	9.0	28.9	24.4	36.2	0.4	67.9	31.7	27.1	173.8	9.9	1.0	12.9	166.7	256.4
1977	55.2	12.9	33.3	112.9	3.2	92.3	31.7	27.1	218.9	9.9	1.0	24.7	309.8	313.3
1978	6.9	0.2	136.2	1.0	0.0	163.6	31.7	27.1	176.4	9.9	1.0	47.4	307.9	293.4
1979	87.0	3.3	253.0	0.0	0.0	140.8	37.5	2.0	128.8	14.8	3.0	27.8	484.0	213.9
1980	271.3	7.9	211.7	52.4	0.0	166.4	8.7	7.8	148.7	40.5	4.2	19.8	709.7	229.7
1981	276.4	16.4	342.2	50.9	0.0	174.0	8.1	15.1	156.9	3.9	0.1	11.1	859.9	195.2
1982	212.3	8.6	450.1	30.1	0.0	139.5	5.1	10.0	265.0	6.3	0.0	7.9	840.6	294.2
1983	114.0	17.4	378.1	6.9	0.0	104.5	18.3	9.7	152.7	0.9	0.1	3.1	621.0	184.7
1984	60.7	17.6	301.5	17.6	0.2	158.5	5.7	67.4	124.4	0.0	1.0	5.6	556.0	204.1
1985	0.0	2.6	231.5	6.8	0.2	142.4	45.4	1.9	167.1	89.9	0.8	9.4	383.5	314.5
1986	8.2	25.8	285.8	6.6	0.0	208.1	13.4	2.6	140.8	0.1	0.0	20.3	534.6	177.1
1987	6.9	19.1	308.3	0.0	0.0	156.5	44.2	16.1	151.0	1.9	0.0	22.6	490.9	235.7
1988	28.2	19.3	369.3	0.2	4.0	146.6	57.8	66.9	157.9	3.3	0.0	10.6	567.5	296.5
1989	0.0	21.1	389.2	0.0	4.9	164.6	37.4	95.1	137.4	0.0	0.0	9.1	579.8	279.0
1990	0.0	80.5	436.8	0.0	16.5	248.4	197.7	13.8	97.5	0.9	0.0	7.3	782.2	317.1
1991	0.0	93.7	324.3	3.3	5.5	173.7	25.6	12.9	122.7	14.5	0.0	7.1	600.6	182.8
1992	0.0	4.4	211.0	2.0	0.2	82.6	29.3	61.3	81.1	3.0	0.0	4.8	300.2	179.6
1993	0.0	14.9	175.0	2.9	8.7	65.6	10.8	18.6	78.5	1.4	4.8	3.2	267.1	117.4
1994	0.0	11.1	189.3	2.2	0.3	53.9	14.7	17.8	67.7	2.5	0.0	2.7	256.8	105.4
1995	0.0	8.4	177.1	4.5	1.4	72.0	3.4	70.0	66.8	1.8	0.4	4.0	263.4	146.2
1996	0.0	6.4	188.4	0.3	0.0	79.8	36.3	17.5	61.2	0.3	5.0	3.7	274.8	124.0
1997	0.0	4.1	172.9	1.1	0.0	90.8	3.6	7.8	49.8	1.3	0.0	4.1	268.8	66.5

Table 4

Primary and alternate catch-in-numbers-at-age matrix for red porgy off the southeastern United States. Matrix is in thousands of fish, is based on fishery-independent age-length keys, and includes 18% (by number) of released recreationally caught fish. Each year's modal age is underlined.

	Age (yr)								
Year	1	2	3	4	5	6	7	8+	Total (1000)
Primary catch-in-numbers-at-age matrix									
1972	13.2	60.7	56.2	55.9	87.3	44.1	23.5	19.0	359.9
1973	13.7	63.0	62.8	64.6	102.4	55.3	36.8	46.3	444.9
1974	13.7	64.8	63.1	58.8	76.9	35.5	21.7	26.0	360.5
1975	16.7	116.5	96.3	51.3	37.4	38.9	28.2	30.3	415.6
1976	13.8	88.3	87.5	60.4	56.4	46.1	32.5	36.7	421.7
1977	12.9	92.7	102.4	88.9	106.0	78.2	60.2	80.5	621.9
1978	15.3	101.0	106.2	88.2	115.6	69.1	46.9	58.0	600.3
1979	13.9	134.4	145.5	90.6	57.9	95.5	78.4	81.0	697.2
1980	14.6	153.9	212.2	128.6	76.6	121.6	100.2	130.9	938.6
1981	16.3	206.5	218.3	215.6	156.6	86.8	55.7	99.2	1055.1
1982	24.7	289.8	246.1	218.6	147.7	76.5	47.3	83.9	1134.8
1983	35.6	128.2	184.0	185.5	98.2	65.6	45.5	63.0	805.7
1984	31.1	137.7	202.5	186.6	85.5	50.8	28.3	37.5	760.0
1985	34.1	116.4	118.1	155.6	127.6	84.3	38.0	24.0	698.0
1986	29.0	143.4	134.9	160.6	118.6	71.3	32.5	22.3	712.7
1987	71.8	227.2	176.9	95.9	38.3	44.4	32.4	39.0	725.8
1988	87.9	288.7	219.0	109.0	42.2	46.8	30.5	38.2	862.4
1989	40.0	232.9	247.2	122.9	92.5	37.5	36.6	46.8	856.3
1990	66.2	325.1	322.5	146.1	105.2	40.2	40.3	49.9	1095.4
1991	46.7	160.4	162.9	181.1	97.5	54.9	29.6	49.9	783.0
1992	19.6	63.7	95.7	124.2	73.3	42.1	22.0	38.9	479.4
1993	3.9	38.9	53.2	95.7	94.7	51.0	24.0	23.2	384.5
1994	3.3	32.5	47.7	89.2	91.0	50.4	24.7	23.5	362.2
1995	5.2	39.9	54.7	98.0	97.2	52.6	23.8	24.1	395.5
1996	4.9	44.9	57.9	99.9	95.6	50.6	21.5	21.1	396.3
1997	2.3	31.9	46.2	85.3	85.2	45.2	20.2	18.8	335.2

continued

headboat catches are shown for comparison, but were not used in calibrating VPAs.)

In the primary catch matrix, modal age (underlined in Table 4) varied between 2 and 5; age 4 has been most common in recent years. Modal age in the alternate catch matrix (Table 4) was similar, but showed less annual variation, probably because of interpolation across years of the age-length keys. A few strong year classes have moved through the population, most notably those that were age 2 in 1987–90, but no strong year classes have followed. The modal age has increased since 1992, the year in which a 12-inch minimum size limit was imposed (amendment 4 [SAFMC[5]]).

Trends in mortality and recruitment

In our calibrated VPAs, ages 4 through 7 were always considered fully recruited, and estimates of F were typically averaged over those ages, weighted by population numbers at age. Those weighted averages are referred to here as full F.

In analysis of the primary catch matrix, estimates of F for all ages were lowest in the early years (Table 5). Fishing mortality on ages 1–3 increased between the early and middle periods and then declined, but full F (ages 4+) increased and remained high. This pattern probably reflects the imposition of the 12-inch TL minimum size limit in 1992 with amendment 4 (SAFMC[5]). Estimates of F from the alternate catch matrix in the recent period were generally higher for ages 3+ than estimates from the primary catch matrix. Slightly lower estimates of F in the recent time period were obtained from the primary catch matrix when missing values, rather than small numbers, replaced zeroes in computing the hook-and-line index.

Estimates of full F from both catch matrices started low, rose abruptly from the late 1970s to 1982, decreased some-

Table 4 (continued)

Year	Age (yr) 1	2	3	4	5	6	7	8+	Total (1000)
Alternate catch-in-numbers-at-age matrix									
1972	13.2	60.7	56.2	55.9	87.3	44.1	23.5	19.0	359.9
1973	13.7	63.0	62.8	64.6	102.4	55.3	36.8	46.3	444.9
1974	13.7	64.8	63.1	58.8	76.9	35.5	21.7	26.0	360.5
1975	18.7	71.0	79.4	78.7	74.7	40.6	21.5	31.7	416.2
1976	15.2	57.6	69.1	79.7	85.8	49.2	26.6	39.0	422.2
1977	14.2	65.6	83.3	105.3	128.4	82.8	52.8	89.9	622.3
1978	16.6	78.5	99.0	102.4	121.2	75.2	43.9	63.7	600.5
1979	15.2	78.2	98.4	116.6	150.7	99.9	59.3	79.7	697.9
1980	15.8	86.0	129.2	171.7	213.4	116.6	70.1	136.6	939.3
1981	12.6	93.9	149.2	197.9	247.8	136.6	86.2	131.2	1055.1
1982	18.7	150.5	191.4	216.7	252.0	122.2	73.9	109.5	1134.8
1983	41.5	132.9	135.4	146.2	162.0	70.3	48.7	69.0	805.8
1984	36.4	145.9	154.0	151.0	153.5	54.5	27.9	36.8	760.1
1985	27.5	120.7	142.0	140.3	156.6	56.3	25.8	28.9	698.0
1986	25.2	120.5	159.5	169.0	131.4	52.3	23.0	31.7	712.7
1987	6.9	88.3	204.0	180.5	129.8	56.4	26.1	34.6	726.6
1988	15.4	111.7	262.3	224.5	141.3	53.8	23.8	31.3	864.0
1989	15.1	132.5	255.2	199.0	140.6	58.5	25.2	32.7	858.8
1990	32.5	216.4	330.7	247.5	158.7	57.7	23.0	32.9	1099.4
1991	22.5	165.6	238.3	180.9	104.5	34.4	14.7	22.6	783.4
1992	10.5	65.6	138.4	129.1	86 9	28.8	9.6	11.0	479.8
1993	1.9	29.8	104.6	125.7	80.5	24.6	8.4	9.1	384.5
1994	1.8	27.2	91.9	119.7	79.7	24.1	9.0	9.0	362.3
1995	3.6	37.7	108.4	128.4	81.1	21.6	6.8	7.9	395.5
1996	0.3	9.1	104.6	142.5	89.8	30.4	9.2	10.6	396.3
1997	0.1	3.3	76.9	125.8	83.9	28.4	8.1	8.8	335.2

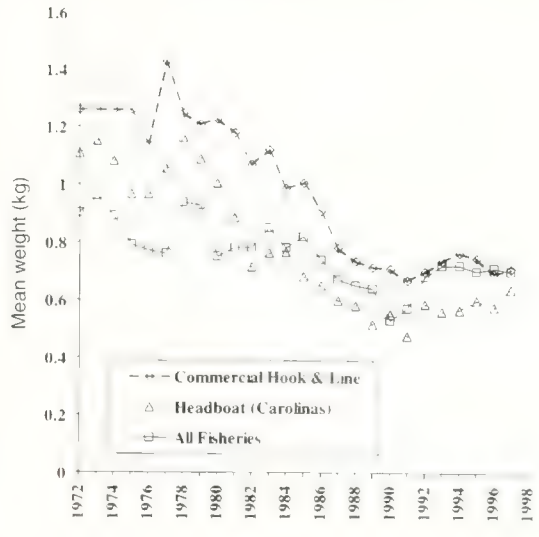

Figure 2

Annual mean weight of red porgy off the southeastern United States in landings from commercial hook-and-line, headboats from the Carolinas, and from all fisheries. Minimum size limit was introduced in 1992.

what, and gradually increased through the present (Fig. 4A). Of the two matrices, the primary matrix provided lower estimates of full F in the recent period, particularly with zeroes replaced by missing values.

Estimates of recruitment were not particularly sensitive to estimation procedure. A general decline in recruitment, 1973–97, was estimated from both catch matrices and with either treatment of zeroes (Fig. 4B).

Sensitivity runs on the primary catch matrix, but with M = 0.20/yr or M = 0.35/yr, estimated that patterns in F and recruitment were similar to those with the base value of M = 0.28/yr (Fig. 5). Under the assumption M = 0.20/yr, estimated values of F were higher than the base assessment; whereas under the assumption M = 0.35/yr, estimated values of F were lower (Fig. 5A). Effect of the value of M on recruitment increased with each year backwards in time. Regardless of the value of M, the pattern of estimates was of initially high recruitment, followed by a long period of severe decline (Fig. 5B).

For comparative purposes, VPA fits were also made by using only the hook-and-line index or only the extended chevron-trap index. Essentially no differences were noted in estimates of full F or recruitment to age 1.

In our VPAs, we estimated statistical weights for the two calibration indices. Estimated weights varied only slightly

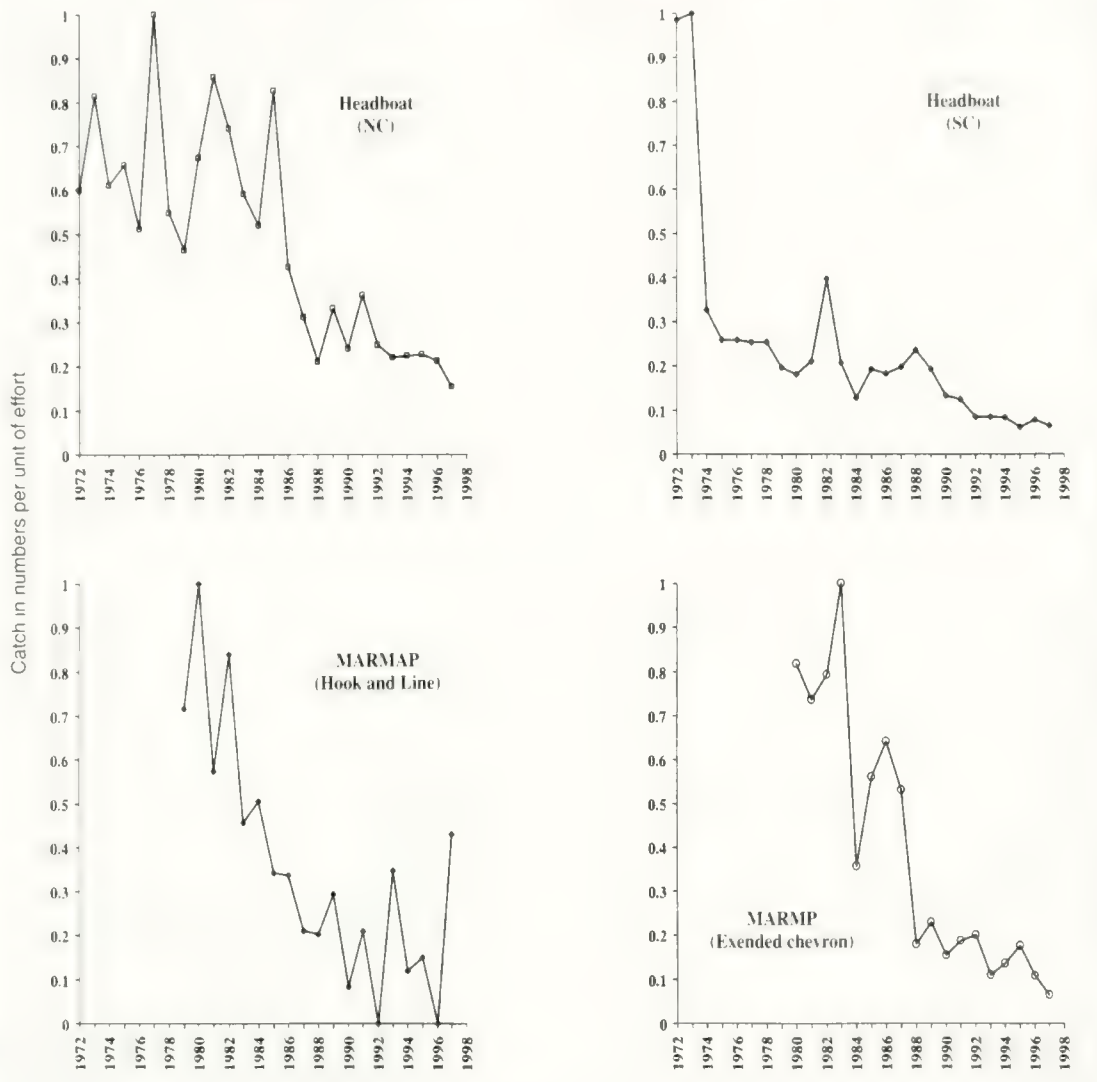

Figure 3

Catch per effort (standardized to series maximum) from the headboat fishery in North and South Carolina (fish caught per angler day, 1972–97); and from MARMAP sampling by gear (hook-and-line, 1979–97; and extended chevron trap, 1980–97), for red porgy off the southeastern United States.

with different assumptions about M. Base analysis of the primary catch matrix estimated weights of 0.08 for hook-and-line CPE and 0.92 for extended chevron-trap CPE; analysis of the alternate catch matrix estimated weights of 0.05 and 0.95. When missing values were used in place of zeroes in the hook-and-line index, estimated weights were 0.50 for hook-and-line CPE and 0.50 for extended chevron trap CPE, demonstrating that treatment of zeroes is an important consideration. The main change in results from using missing values was decreased estimates of F in recent years (Fig. 4A).

In the retrospective analysis, estimates of F generally converged in about 3 to 4 years; convergence in estimates of recruitment took a year or two longer (Fig. 6). A large positive retrospective pattern was evident in full F in the most recent year, and a corresponding negative pattern in estimates of recruitment (Fig. 6). The retrospective pattern was similar when using missing values for zeroes.

Yield per recruit and related benchmarks

Estimates of equilibrium YPR were somewhat sensitive to the value of M assumed, with larger assumed values of M corresponding to smaller estimates of YPR. The highest YPR was obtained during the middle time period (Table 6); however, high theoretical values of yield per recruit can result from fishing mortality rates that are not sustainable.

The two biological reference points F_{max} and $F_{0.1}$ (Beverton and Holt, 1957; Sissenwine and Shepherd, 1987) were estimated from the yield-per-recruit analysis. Assuming

partial recruitment based on average F at age, these reference points were estimated for the recent time period from the primary and alternate catch matrices as F_{max} = 0.5/yr and 0.7/yr, respectively; and $F_{0.1}$ = 0.23/yr and 0.25/yr, respectively (Table 7).

Spawning potential ratio, spawning-stock biomass, and stock-recruitment model

Estimates of static SPR were calculated by catch matrix, time period, and assumed value of M and for four measures of spawning biomass (total mature biomass, mature female biomass, mature male biomass, and egg production) (Table 6; Fig. 7). Static SPR based on mature female biomass was less affected by increases in F than static SPR based on mature male biomass because younger fish are predominantly female and older fish, male. For example, full F that produced 59% SPR in mature female biomass produced 49% SPR in egg production, 42% SPR in total mature biomass, and 27% SPR in mature male biomass (Table 6).

Corresponding estimates were made of reduction in the proportion of males due to fishing in the three periods. For example, a value of 69% in the last column of Table 6 means that if the proportion of males in the mature unfished population had been 50%, introduction of fishing mortality would reduce this proportion to 34.5% of the population (69% × 50%). These estimates were made on the basis of observed sex ratios at size and assuming that the rate of transformation from female to male does not increase as the population is fished down.

Total spawning stock biomass (SSB) was estimated from the primary catch matrix to have reached its peak in about 1979 at 3530 t, declining to 397 t in 1997 (Fig. 8A). When missing values were substituted for zeroes in computing the CPE index, estimates of SSB near the end of the series were slightly higher (Fig. 8A). Estimates from the alternate matrix were similar, with the largest differences occurring before 1983 (Fig. 8A).

Static SPR estimated from the primary catch matrix was high during the 1970s, reached 67% in 1975, and declined to a minimum of 33% in 1982, increased again to 55% in 1993, and declined to about 18% in 1997 (Fig. 8B). Estimates from the alternate catch matrix were similar, but markedly lower from 1983 to 1994 (Fig. 8B). Values of full F providing spe cified values of static SPR (based on female egg production and total spawning stock biomass) are summarized in Table 7, along with values of full F averaged by period, for comparative purposes.

The recent management definition of overfishing is static SPR <35% (amendment 12 [SAFMC[3]]). Our primary estimates are of static SPR >35% from 1972 to 1994 (except for 1982), lower thereafter. Estimates from the alternate catch matrix show static SPR >35% from 1972 to 1980, lower thereafter.

During the early to mid 1970s, a large spawning stock produced high recruitment. Despite a high spawning-stock size estimated through about 1983, SPR and recruitment declined, and the unsustainable landings of the late 1970s and 1980s reduced the spawning stock to levels not expected (under the stock–recruitment model) to provide good recruitment. Similar patterns were apparent in stock-recruitment curves derived from both catch matrices (Fig. 9).

Table 5

Mean estimates (from calibrated virtual population analyses) of age-specific instantaneous fishing mortality rate (F) on red porgy off southeastern U. S. during three time periods. Estimates from primary catch matrix (see text) are given for three levels of natural mortality rate M, two treatments of missing values for M=0.28. Estimates from alternate catch matrix given for M = 0.28 only. Exploitation rate in final column is based on catch of ages 1–8 divided by estimated population number of same ages.

	Age (yr)				Exploitation rate
Analysis	1	2	3	4+	(ages 1–8)
Primary (MARMAP) catch matrix					
(M=0.28)					
1972–78	0.007	0.06	0.08	0.15	0.06
1982–86	0.018	0.12	0.19	0.35	0.12
1992–96	0.014	0.10	0.15	0.44	0.16
(M=0.28, zeroes in index treated as missing)					
1972–78	0.007	0.06	0.08	0.15	0.06
1982–86	0.018	0.12	0.19	0.35	0.12
1992–96	0.011	0.08	0.13	0.40	0.14
(M=0.20)					
1972–78	0.010	0.08	0.11	0.20	0.08
1982–86	0.025	0.16	0.24	0.43	0.16
1992–96	0.017	0.12	0.17	0.49	0.19
(M=0.35)					
1972–78	0.005	0.04	0.06	0.11	0.04
1982–86	0.013	0.09	0.14	0.28	0.09
1992–96	0.012	0.09	0.14	0.40	0.14
Alternate catch matrix					
(M=0.28)					
1972–78	0.006	0.04	0.06	0.14	0.05
1982–86	0.017	0.10	0.18	0.42	0.13
1992–96	0.007	0.06	0.27	0.66	0.18

Estimates of benchmarks from simulations

Estimates of MSY, B_{MSY} and F_{MSY} were made from the stock–recruitment model and age-structured simulations (Table 8; Fig. 10). In addition, minimum stock size threshold (MSST), a benchmark recently introduced into U.S. Federal fishery management, was calculated from B_{MSY} as suggested in Restrepo et al. (1998), namely as MSST = $(1-M)\ B_{MSY}$, with M = 0.28/yr. Although benchmarks are somewhat sensitive to assumptions examined, sensitivity was small compared with the difference between estimated benchmarks and current status of the stock and fishery (Table 8). For example, estimates of MSY obtained in this way (240–280 t/yr) were similar to recent landings (about

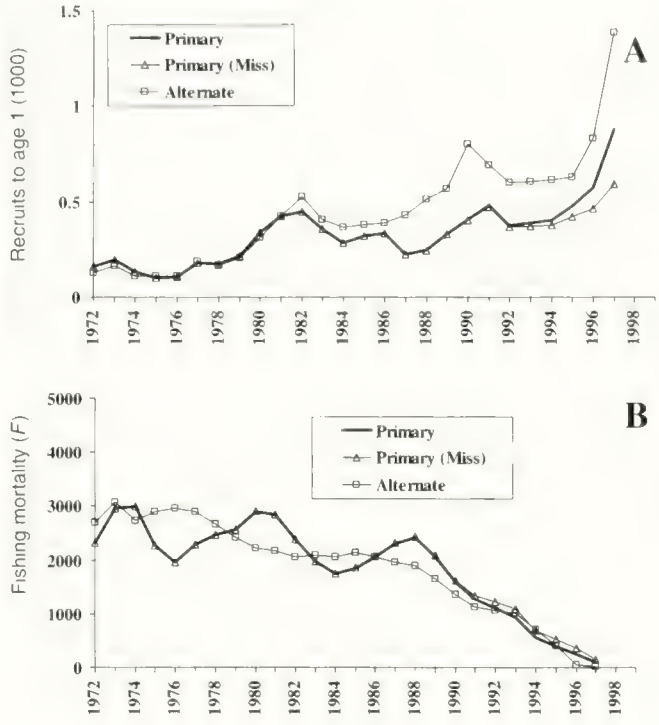

Figure 4

(**A**) Annual estimated instantaneous fishing mortality rates (mean F on ages 4–8), and (**B**) recruitment to age 1 from calibrated VPA applied to red porgy off southeastern United States based on different catch matrices and treatment of zeroes (alternative treatment of zeroes as missing value is indicated as "Miss" after Primary) in MARMAP hook-and-line CPUE.

200–300 t/yr), but well below landings taken earlier (e.g. >800 t in 1981 and 1982). Estimates of fishing mortality rates in the recent period are about 2.7 to 3.6 times those that could produce MSY (Table 8). Because benchmark estimates are based on selectivity patterns estimated for 1992–96, their values are expected to change with the recent introduction of higher minimum size limits. However, the general picture is unlikely to change.

Surplus-production model

It was not possible to estimate the shape parameter of the generalized production model from these data; therefore, we present results only for the logistic model. Fits of that model with various assumptions about B_1/K were statistically equivalent (log likelihoods from –2.29 to –2.25), indicating that the data–model combination is not informative about relative biomass level at the start of the time series. We present results under a range of assumptions centered on $B_1/K = 0.75$ (Table 9). The estimate of MSY was moderately sensitive to the assumption on B_1/K, varying about 18.5% around the central estimate (Table 9); it was also higher than our estimates from age-structured methods (Table 8). Nonetheless, the bias-corrected 80% confidence interval on the central MSY estimate (Table 9) and the corresponding 50% interval (not shown) included the age-structured estimates of MSY; therefore there was some agreement between methods.

Estimates of stock and fishery status expressed in relative terms (Table 9) were similar to those from the age-structured analysis (Table 8) and like those estimates depicted a heavily overexploited stock. Stock biomass at the start of 1998 was estimated as about 25% of the biomass that can support MSY (B_{MSY}), a result that was remarkably insensitive to the assumption on B_1/K. Fishing mortality rate in 1997 was estimated as about twice the fishing mortality rate associated with MSY (F_{MSY}), a result only slightly sensitive to the assumption on B_1/K. Equilibrium yield available in 1998 was estimated as about 44% of MSY; this reduction was due to the stock's reduction well below B_{MSY}.

Estimates of relative stock and fishery status over time displayed a pattern of increasing fishing mortality rate and decreasing abundance over time (Fig. 11). It appears that the biomass moved below B_{MSY} in about 1982 and that the fishing mortality rate has been above F_{MSY} since about 1978. Estimated confidence intervals on F/F_{MSY} are remarkable in encompassing a wide range that since

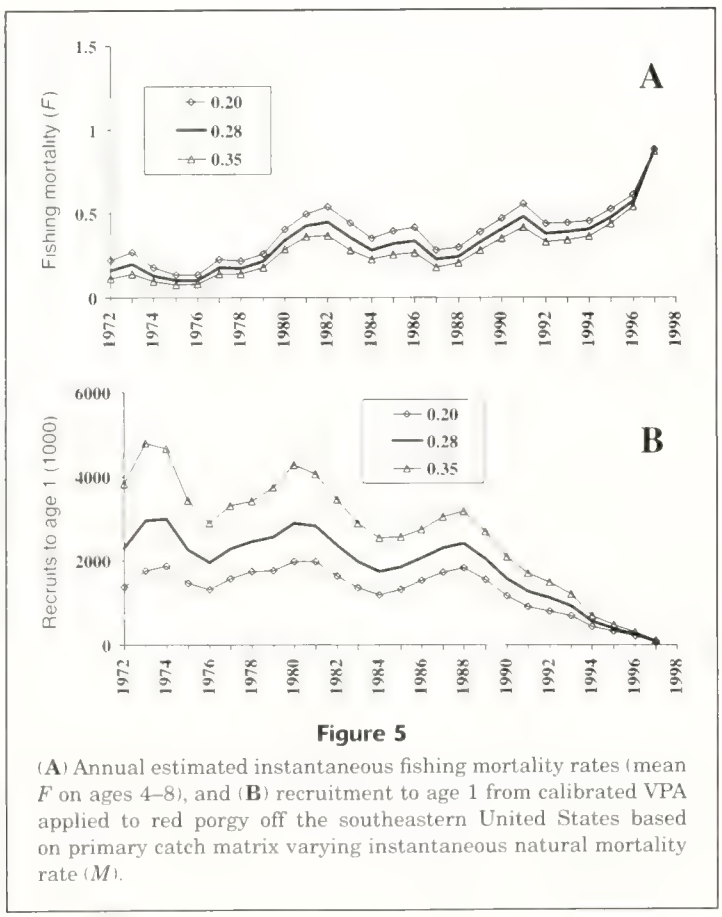

Figure 5

(**A**) Annual estimated instantaneous fishing mortality rates (mean F on ages 4–8), and (**B**) recruitment to age 1 from calibrated VPA applied to red porgy off the southeastern United States based on primary catch matrix varying instantaneous natural mortality rate (M).

about 1980 has included only values greater than unity (Fig. 11B).

Discussion

This work includes numerous advances from previous assessments (Vaughan et al., 1992; Huntsman et al.[1]). The major improvements are availability of additional fishery-dependent and fishery-independent aging data and of fishery-independent indices for calibrating VPAs. Other changes include expanded geographic range, new estimates of sex ratios and maturity schedules, new growth parameters, application of a more modern algorithm for calibrated VPA, and application of a nonequilibrium surplus-production model. Our conclusions agree with both earlier assessments in finding a population in decline.

Because unbiased sampling of wild fish stocks is extremely difficult and fishery data sets are small (in number of years of data), fish population models are not precise approximations of reality. Accurately characterizing uncertainty in assessment results is difficult or impossible: although statistical estimates of uncertainty can be obtained, it is not known how to balance them against factors that tend to increase certainty, such as agreement among data sources or methods and among assessments conducted over time. Any formal estimate of uncertainty in the present assessment results would be large. Nonetheless, in light of our use of complementary models, several independent data sources, and two largely independent sets of age-length keys, and based on agreement with past assessments, we believe that the present results are unequivocal in their major finding of a severely depleted population.

By using two treatments of observed zeroes in CPE series, we illustrated that some results can be sensitive to the method used to treat zeroes. Although addition of a constant before logarithmic transformation is a widely used practice and has been a common statistical recommendation (e.g. Snedecor and Cochran, 1980; Berry, 1987), it is becoming evident that the practice can be problematic in estimation of abundance indices. Logarithmic transformation is made under the assumption of lognormally distributed data, and presence of zeroes in itself violates that assumption. Moreover, results can depend strongly on the additive constant chosen (Porch and Scott, 1994; Ortiz et al., 2000). The root of the problem is that transformed zeroes are usually extreme values in the data set and thus highly influential. Several other statistical models have been proposed, of which the most promising in this application may be the delta–lognormal model (Lo et al., 1992; Ortiz et al., 2000). However, this is still an active area of methodological research, and the matter remains unresolved. We thus used two treatments of zeroes and have

Table 6

Static yield per recruit (YPR) and spawning potential ratio (SPR) of red porgy off southeastern United States. Estimates are based on mean age-specific fishing mortality rates from calibrated VPA on primary or alternative catch matrices (see text), are made under several assumptions about natural mortality rate, M, and treatment of missing values in hook-and-line abundance index, and use selectivity for most recent time period, (1992–96).

Analysis	YPR (g)	Spawning potential ratio				Percentage of males in relation to no fishing[1]
		Total	Female	Eggs	Male	
Primary (MARMAP) catch matrix						
(M=0.28)						
1972–78	152.3	61	74	67	49	83
1982–86	214.3	40	58	47	26	71
1992–96	162.2	42	59	49	27	69
(M=0.28, zeroes in index treated as missing)						
1972–78	152.3	61	74	67	49	83
1982–86	214.2	40	58	47	26	71
1992–96	160.9	44	61	51	29	70
(M=0.20)						
1972–78	263.5	43	60	49	33	74
1982–86	306.6	25	43	31	15	61
1992–96	229.5	29	47	37	17	60
(M=0.35)						
1972–78	89.8	74	84	78	63	89
1982–86	149.5	54	69	60	39	78
1992–96	118.7	52	67	58	36	75
Alternate catch matrix						
(M=0.28)						
1972–78	145.1	64	77	70	53	84
1982–86	261.4	33	53	37	20	69
1992–96	198.2	27	46	33	14	64

[1] Percent relative reduction in numbers of mature males between fished and unfished conditions; i.e. proportion of males under fished conditions is x% of proportion of males under unfished conditions.

presented both sets of results, which are different, but not remarkably so.

Several issues arise from choosing as "primary" the catch matrix developed from fishery-independent age data and as "alternate" the matrix from fishery-dependent data. The choice was by necessity somewhat subjective, but was based on the long-term (1979–94), continuous nature of the fishery-independent data on age at size and its larger sample sizes, in contrast to the intermittent age sampling in the fishery, which required frequent interpolation of age-length keys to construct the alternate catch matrix. The different selectivity of the fishery-independent gear should not significantly bias the primary catch matrix, but fishery-independent samples at larger sizes were sometimes very small, making it necessary to pool data across longer periods for the largest sizes. Parallel analyses were conducted with the two catch matrices to determine sensitivity of major results to the choice of matrices as primary and alternate.

Size selectivity of the gear can have much greater effect in fitting growth models. Fishery-dependent sampling, by selecting larger fish, may overestimate mean size at younger ages, but estimate L_∞ more accurately, whereas fishery-independent sampling, by selecting smaller fish, may underestimate L_∞. In a simulation study, Goodyear (1995) noted: ". . . samples drawn from size-selective gears or fisheries yield biased estimates of mean length at age. . . . Even slight changes in sampling protocol can result in misleading temporal shifts of estimates of size at age." This aspect of the differing selectivity between gears seems important to us, and it can bias estimation of growth models. As a result, we cannot say whether estimated temporal differences in size at older ages result from changes in growth patterns in response to long-term overexploitation (Harris and McGovern, 1997) or from a change in sampling-gear selectivity in the fishery-independent sampling gear (Potts et al., 1998).

Despite questions about size at age over time, patterns of population benchmarks and stock status estimated from

Table 7

Potential biological reference points developed from static yield per recruit (YPR) and spawning potential ratio (SPR) analyses for red porgy off southeastern United States estimated from output from calibrated VPA using selectivity for most recent time period (1992–96), and based on primary catch matrix (three levels of M, and run with missing value for 0.0 in parentheses) or alternate catch matrix (M=0.28). See text for derivation of catch matrices.

	Primary catch matrix				Alternate catch matrix
	M=0.20	M=0.28	M=0.28 (missing)	M=0.35	M=0.28
Yield per recruit (YPR) analysis					
$F_{0.1}$	0.15	0.23	(0.23)	0.31	0.25
F_{max}	0.25	0.53	(0.56)	0.84	0.72
Static spawning potential ratio analysis (static SPR)					
Female (eggs)					
F_{30}	0.25	0.49	(0.50)	0.79	0.77
F_{40}	0.20	0.37	(0.38)	0.60	0.55
F_{50}	0.17	0.29	(0.30)	0.46	0.41
Total spawning-stock biomass					
F_{30}	0.25	0.42	(0.43)	0.69	0.51
F_{40}	0.20	0.33	(0.34)	0.52	0.38
F_{50}	0.17	0.26	(0.27)	0.40	0.30
Observed full F by period					
1972–78	0.20	0.15	(0.15)	0.11	0.14
1982–86	0.43	0.35	(0.35)	0.28	0.42
1992–96	0.49	0.44	(0.40)	0.40	0.66

Table 8

Parameters and potential biological reference points developed for Beverton-Holt spawner-recruit model of red porgy off southeastern United States. Estimates are based on calibrated VPA by using selectivity for most recent time period (1992–96), and based on primary catch matrix (fishery-independent keys; includes separate run with missing value for zeroes in hook-and-line index) or alternate catch matrix (fishery-dependent keys).

Parameter estimate or reference point	Primary catch matrix	Primary CM (missing)	Alternate catch matrix
Parameter estimates (standard error in parentheses)			
b_0	1.83×10^{-4}	2.01×10^{-4}	2.32×10^{-4}
	(7.0×10^{-5})	(6.7×10^{-5})	(5.3×10^{-5})
b_1	0.669	0.617	0.605
	(0.185)	(0.175)	(0.157)
$\max(R_1) = 1/b_1$	5.46×10^6	4.98×10^6	4.31×10^6
Reference points			
MSY	242	248	277
F_{MSY}	0.14	0.15	0.18
B_{MSY}	2564	2425	2387
MSST	1846	1746	1719
Estimates of SSB (spawning stock biomass) by period			
1972–78	2884	2885	3367
1982–86	2326	2330	2651
1992–96	876	953	669
Estimates of stock status			
$F_{1992-96}/F_{MSY}$	3.2	2.7	3.6
$B_{1992-96}/B_{MSY}$	0.34	0.39	0.28

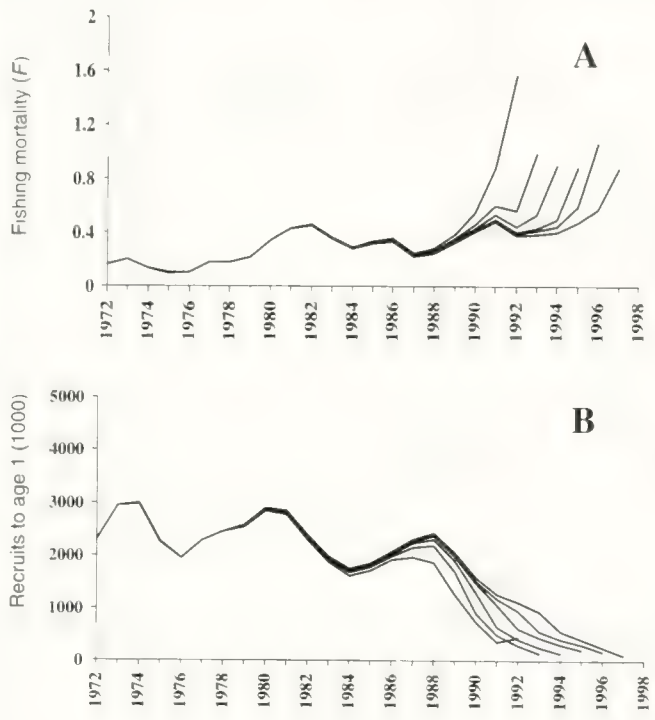

Figure 6

Retrospective patterns in (**A**) annual estimated instantaneous fishing mortality rates (mean F on ages 4–8), and (**B**) recruitment to age 1 from calibrated VPA applied to red porgy off southeastern United States based on primary catch matrix with earlier final year compared to analysis with the most recent final year (1997).

Table 9

Estimates of biological benchmarks and stock status from application of logistic surplus-production model to red porgy off the southeastern United States. Symbols are B_1 = biomass in first year; K = carrying capacity; MSY = maximum sustainable yield; B_{98}/B_{MSY}= biomass at start of 1998 (year following analysis) relative to biomass at MSY; F_{97}/F_{MSY} = fishing mortality rate in 1997 compared with F at MSY; Ye_{98} = equilibrium yield available in 1998. Because B_1 could not be estimated with any precision, the model was fitted under a range of assumptions on its value in relation to that of K. For central case, 80% confidence intervals are shown in parentheses.

Benchmark or status indicator	Assumed value of B_1/K				
	0.55	0.65	0.75	0.85	0.95
MSY (t/yr)	506	482	459 (98–555)	437	416
B_{98}/B_{MSY}	0.247	0.247	0.248 (0.116–0.373)	0.250	0.252
F_{97}/F_{MSY}	1.85	1.93	2.01 (1.36–5.08)	2.09	2.17
Ye_{98} (t)	219	209	199 (69.0–304)	191	183
Ye_{98}/MSY	0.434	0.433	0.434 (0.219–0.607)	0.437	0.440

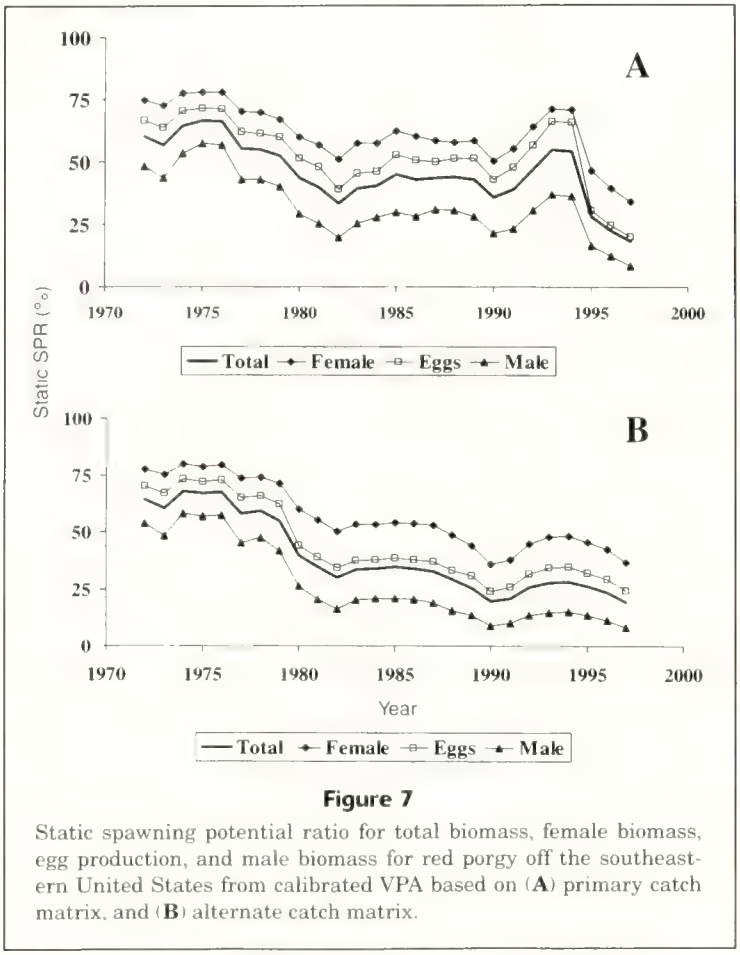

Figure 7

Static spawning potential ratio for total biomass, female biomass, egg production, and male biomass for red porgy off the southeastern United States from calibrated VPA based on (**A**) primary catch matrix, and (**B**) alternate catch matrix.

the two matrices (and, indeed, in all sensitivity runs) were similar, depicting much higher population size and spawning biomass during the 1970s and severe decline through the 1980s and 1990s. This pattern was independent of the large retrospective pattern in the terminal year. Declining trends in CPE from headboats and in fishery-independent sampling (Fig. 3), combined with the observed decline in recruitment (Fig. 4B), also depict an increasingly depleted population. Additional evidence is provided by the surplus-production model, which estimated that the population was at high levels during the 1970s, but that since the mid 1980s it has been far below the level capable of producing MSY (Fig. 11). Implementation of a 12-inch minimum size limit in 1992 (amendment 4 [SAFMC[5]]) appears to have reduced F only on ages 1–3, but F on fully recruited ages (4+) has increased (Table 5).

Static SPR (in total mature biomass) is estimated for the recent period at 42% and 27% from the primary and alternate catch matrices, respectively (Table 6). Mean SPR estimated from the primary catch matrix for all three periods is above SPR=35%, the value used by the South Atlantic Fishery Management Council to define overfishing for red porgy (amendment 12 [SAFMC[3]]). Estimated SPR from the alternate catch matrix is below 35% in the recent period (Table 6).

Coleman et al. (1999), in a discussion of reef fish management, pointed out that SPR as usually estimated from female biomass or egg production has proven less effective for protogynous reef fishes than for fishes that do not change sex. With the loss of the largest size classes, predominantly male, remaining males may not be able to increase harem size sufficiently to fertilize all available females. Thus, determining SPR solely on female reproductive contribution may not capture the true decline in reproduction caused by fishing. For that reason, Vaughan et al. (1992, 1995) recommended calculating static SPR from total mature biomass, broadening the concept of static SPR for protogynous species. Vaughan et al. (1995) calculated reduction in the proportion of males for black sea bass due to changes in fishing mortality and under the assumption that transition rate does not change with population abundance. They estimated a reduction of about 40% due to recent fishing mortality, a reduction similar to the ~30% we estimated for red porgy.

Whether males are currently limiting, or the degree to which increased fishing mortality can cause them to become limiting, is unknown. Regardless, increased fishing mortality on all ages would be expected to reduce the proportion of males in the mature population. The rate at which the imposition of fishing mortality may alter the av-

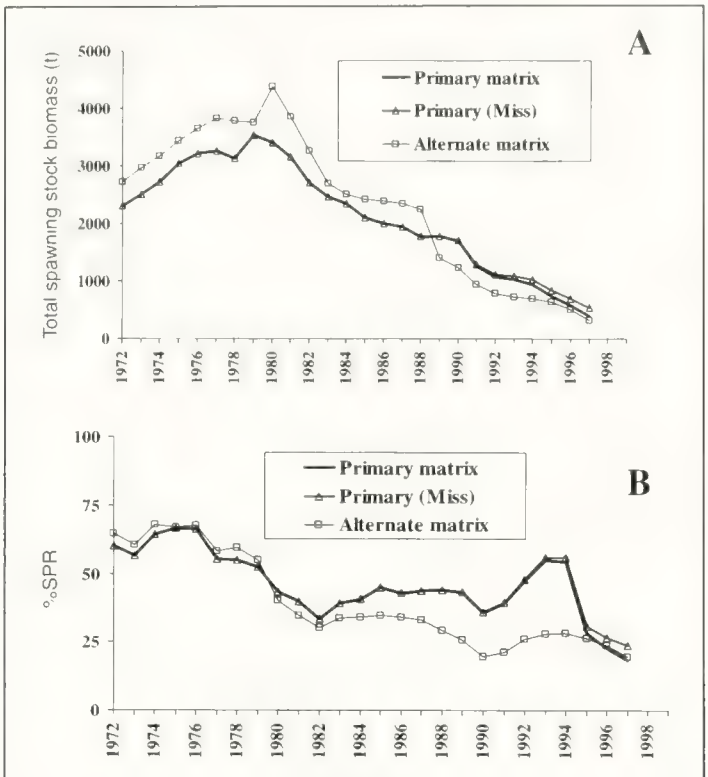

Figure 8

Annual estimates of (**A**) total spawning stock biomass, and (**B**) static spawning potential ratio (SPR) for red porgy off the southeastern United States from calibrated VPA based on different catch matrices and treatment of zeroes (alternative treatment of zeroes as missing value is indicated as "Miss" after Primary) in MARMAP hook-and-line CPUE.

erage age of transition to male is unknown, as is the effect of population density on transformation rate.

Increased sex transformation due to reduced abundance of males, as reported in other protogynous reef fish (Shapiro, 1979), would cause declines in mature female biomass and egg production beyond those expected from fishing alone. McGovern[7] found a greater percentage of males in smaller size classes in 1991–99 than in 1979–81 and suggested that red porgy have compensated for the loss of large individuals by becoming male at smaller sizes. If so, a smaller change in sex ratio, but a greater reduction in egg production, would be expected than implied by increasing fishing mortality alone.

New evidence suggests that red porgy are indeterminate, serial spawners (Daniel[8]). That is, the size and number of batches of eggs are not fixed at the start of the spawning season, but older, larger females spawn in larger batches, more frequently, and possibly over a longer season than younger, smaller females. If so, SPR based on egg production estimated from a fixed weight–fecundity relationship would be unrealistic, and SPR based on total mature biomass would underestimate the contribution of older fish, and thus underestimate the effects of fishing.

Huntsman and Schaaf (1994) proposed accounting for sex-composition changes by multiplying total egg production by a factor representing the probability of successful fertilization. They calculated that probability (Q) for a given fishing mortality rate F^* from the relative change in male contribution of spawning products under fishing:

$$Q = \frac{(G_m / G_f) \mid F = F^*}{(G_m / G_f) \mid F = 0},$$

where G_m and G_f = the gamete contributions of males and females, respectively.

Huntsman and Schaaf (1994) computed G_m as total male biomass and G_f as total female egg production. When new information on red porgy batch spawning becomes avail-

[7] McGovern, J. C. 2001. Personal commun. South Carolina Department of Natural Resources, P.O. Box 12559, Charleston, SC 29422.

[8] Daniel, E. A. 2001. Personal commun. University of Charleston, Charleston, SC 29424.

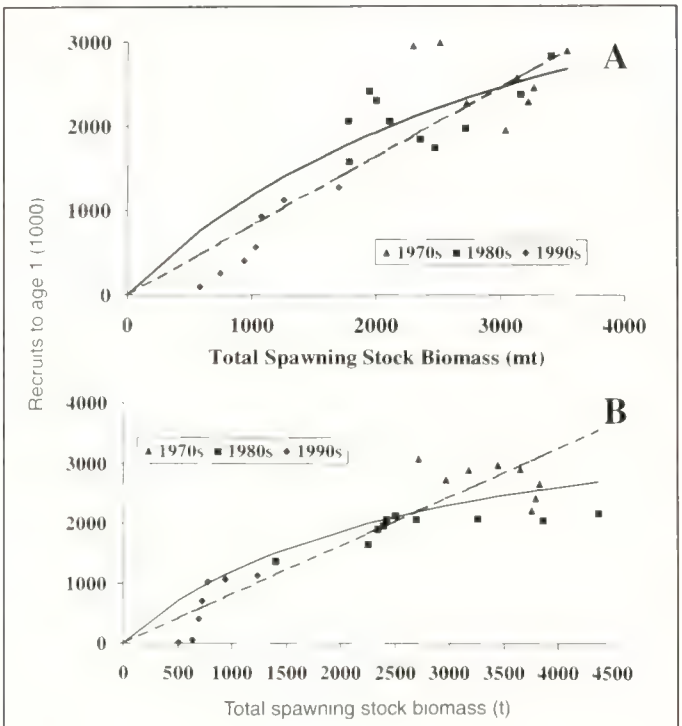

Figure 9

Total spawning-stock biomass and recruitment to age 1 for red porgy off the southeastern United States from calibrated VPA based on (**A**) primary catch matrix, and (**B**) alternate catch matrix. Solid lines represent recruitment predicted from Beverton-Holt models; dashed lines run from the origin with slope of median of recruits divided by the spawning-stock biomass for 1972–94 spawning years.

able and allows calculation of total population fecundity at Z and M, we recommend exploring that approach. Population simulations for a protogynous grouper (Huntsman and Schaaf, 1994) suggest greater vulnerability to fishing than for a comparable gonochoristic stock. It appears that the questions of what SPR measure is most appropriate and how it should be computed cannot be answered until the overall reproductive biology of the species is far better understood.

As usual for fish populations, the spawner–recruit relationship is only roughly defined by the data (Fig. 9), and the years in which the model does not fit raise interesting questions. In the fit based on the primary catch matrix (Fig. 9A), the two large residuals at the start might be taken as suggestive of a dome-shaped recruitment curve, they simply might reflect random error, or they might result from the additional computations needed to extend the catch matrix back to 1972. The analysis based on the alternate catch matrix (Fig. 9B) shows a more pronounced pattern, in which data from the 1970s demonstrate higher recruitment for a given level of spawning-stock size than later data. This pattern might be taken as evidence of a regime shift (change in underlying ecological conditions, from natural or anthropogenic causes), or it might be an artifact of the smaller data sets of age-length data used in this approach. Other explanations are equally possible for residual patterns in Figure 9, A and B. These observed data suggest "depensation" (reverse compensation;decreased, rather than increased, recruitment per spawner at lower population sizes) at very low spawning biomasses, but this suggestion is uncertain because of high retrospective error in estimating recruitment in the most recent years.

Growth overfishing was not estimated to be severe. Mean full F in the early period was estimated well below both F_{max} and $F_{0.1}$. Mean full F in the middle period was estimated as about 152% of $F_{0.1}$, and mean full F for the recent period was estimated as about 191% of $F_{0.1}$, both below F_{max} (Table 7). This stock appears to be one in which recruitment overfishing can be induced before growth overfishing, and for that reason reference points such as F_{max} and even $F_{0.1}$ would be insufficiently conservative for its management.

The estimate of B_{MSY} computed from the recruitment model and selectivity vector can be an appropriate target biomass for management and the corresponding MSST can be a threshold to define overfished status (Restrepo et al., 1998). Estimates of spawning-stock biomass were well above MSST, 1972–78; approached MSST, 1982–86; and were well

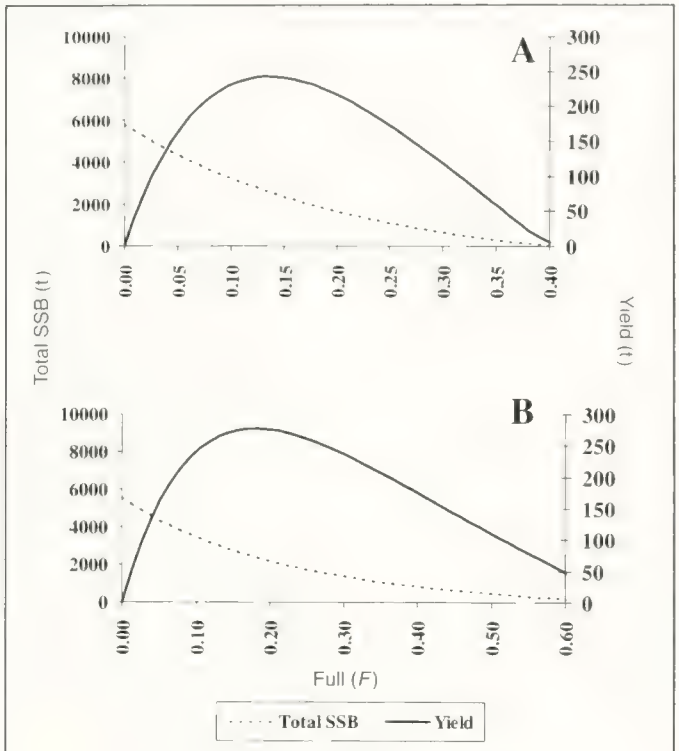

Figure 10

Sustainable yield and spawning stock biomass at varying levels of fishing, projected for red porgy off the southeastern United States from selectivity pattern estimated for 1992–96. Selectivity pattern estimated through calibrated VPA of (**A**) primary catch matrix, (**B**) alternate catch matrix.

below MSST, 1992–96 (Table 8). Still lower estimates of spawning-stock biomass were obtained for the terminal year, although we view terminal-year estimates with scepticism because of retrospective patterns. The production model, not commonly subject to such retrospective patterns, also estimates current biomass as well below MSST (Table 9).

Current estimates of full F (Table 5 for 1992–96) are considerably higher than estimates of F_{MSY} (Tables 8 and 9). In addition, estimates of F_{MSY} are considerably lower than F values corresponding to static SPR of 30% to 40%. If static SPR is used as a reference point, a value higher than SPR = 40% will be necessary to maintain the stock at reasonably productive levels.

It seems inescapable that heavy fishing mortality has been a major cause of the decline in recruitment (Fig. 4B), particularly in the late 1970s and 1980s. Although fishing mortality was lower in the mid-1980s, it increased again in the 1990s for fully-recruited ages (Fig. 4A), and thus static SPR has also declined (Fig. 7). Patterns of increasing F and declining SPR are even more pronounced in estimates from the alternate catch matrix (Figs. 4A, 7). Even though spawning-stock biomass remained high in the late 1970s, recruitment began to decline (Fig. 9). This finding suggests that the usual effects of heavy fishing pressure may have been compounded by other population-specific factors (e.g. those relating to sex structure) or extrinsic factors (e.g. unfavorable environmental conditions) affecting the reproductive success of the population.

Management of hermaphroditic reef fishes is difficult, and it has had few successes (Coleman et al., 1999). As we have shown, interaction of a population's size and sex structures complicates the attempt to model reproductive capacity (e.g. SPR) as a function of fishing mortality rate. Size limits can have subtle side effects if they result in a deficit of males and if larger females in the population consequently change sex at a higher rate. Use of bag limits and size limits in management makes it likely that fish will be caught and released, imposing discard mortality that is incompletely observable. Discard mortality has been found an important factor in collapse of at least one fish stock (Myers et al., 1997). Fish that aggregate become more catchable (increased catchability coefficient $q = F/f$) as abundance declines, another phenomenon associated with risk of collapse (Clark, 1974; Gulland, 1975). Ludwig (1998) has suggested on theoretical grounds that the best management strategy for stocks that may collapse is rapid adjustment of harvest size in response to changes in stock abundance. Ludwig noted: "It is noteworthy that the com-

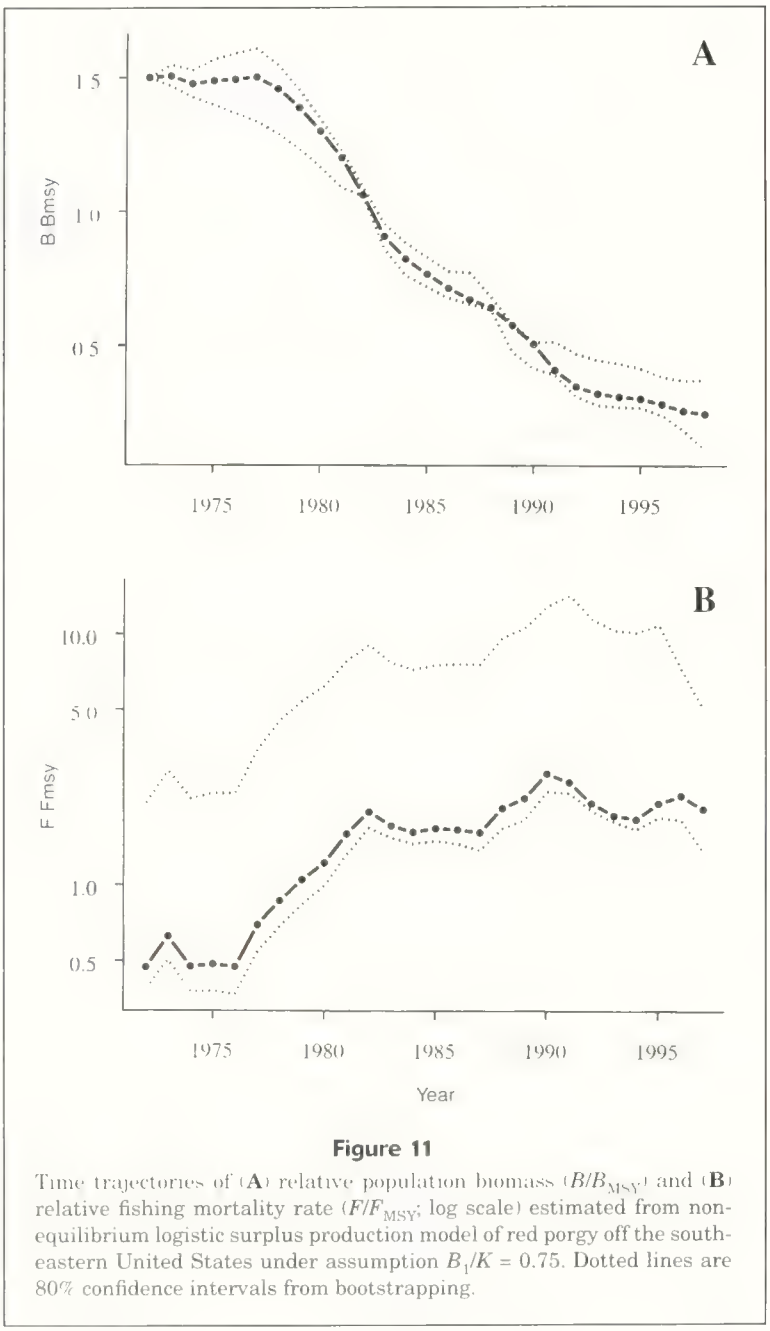

Figure 11

Time trajectories of (**A**) relative population biomass (B/B_{MSY}) and (**B**) relative fishing mortality rate (F/F_{MSY}; log scale) estimated from non-equilibrium logistic surplus production model of red porgy off the southeastern United States under assumption $B_1/K = 0.75$. Dotted lines are 80% confidence intervals from bootstrapping.

plications in stock dynamics all have the same effect upon performance of [management] strategies: they all may cause drastic increases in the probability of extinction and decreases in the expected discounted total yield." It was in the face of such difficulties and uncertainties that the concept of precautionary management was developed (FAO, 1995).

In conclusion, as of 1997 the stock of red porgy off the southeastern United States appears to be in poor condition and getting worse. Even after allowing for retrospective patterns and regardless of catch matrix, estimates are of long-term declines in spawning-stock biomass, recruitment, and catch per effort in the headboat fishery and in fishery-independent surveys. Such estimates strongly suggest overexploitation—overexploitation at an unsustainable rate. Static SPR since 1985 has generally been above the present criterion for overfishing (SPR > 35%), based on estimates from our primary catch matrix. (Estimates from the alternate catch matrix are lower, and estimates from that matrix are generally even more pessimistic about stock status.) During that period, recruitment and spawning stock have continued to decline. Given the present low population level and poor recruitment, we believe that substantial reductions in fishing mortality rate will be necessary to re-

build the stock, whether or not factors other than fishing have contributed to the decline. The situation may be analogous to that of striped bass (*Morone saxatilis*) off the U.S. Atlantic coast in the 1980s, a population that was extremely depressed, with landings reduced by about 75% from their peak. Models of that decline suggested that sharp reductions in fishing mortality would increase the population's growth rate, regardless of the relative importance of fishing and environmental conditions in the preceding decline. Under vigorous management (with sharp reductions in fishing mortality) the population has made a remarkable recovery (Richards and Rago, 1999).

Since completion of this assessment, the South Atlantic Fishery Management Council has taken several actions to promote recovery. As noted in amendment 12 (SAFMC[3]), amendment 9 to the FMP increased the red porgy minimum size limit to 14-inch total length, established a bag limit of 5 fish per person per day, prohibited purchase or sale of red porgy during March and April, and restricted commercial harvest to the recreational bag limit during those months. Subsequently, a prohibition on landing red porgy (moratorium) was enacted for the period 8 September 1999 through 28 August 2000. Amendment 12 (SAFMC[3]) to the FMP, which became effective on 29 August 2000, reduces the recreational bag limit to 1 fish per person per day, extends the closed season to 4 months (January–April), and allows a 50-pound trip limit for commercial landings during the remaining 8 months of each year. Furthermore, the maximum fishing mortality threshold (MFMT) was increased from SPR = 30% (amendment 4 [SAFMC[5]]) to SPR = 35% (amendment 12 [SAFMC[3]]). It remains to be seen whether these actions will be sufficient to achieve the recovery of red porgy.

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A nearsurface, daytime occurrence of two mesopelagic fish species (*Stenobrachius leucopsarus* and *Leuroglossus schmidti*) in a glacial fjord

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The northern lampfish (*Stenobrachius leucopsarus*, family Myctophidae) and northern smoothtongue (*Leuroglossus schmidti*, family Bathylagidae) are mesopelagic fishes, defined by their vertical distribution in the mesopelagic zone (200–1000 m) during daylight hours. Northern lampfish range from the Bering Sea to southern California (Shimada, 1948), where their abundance is highest along the continental slope and decreases over the continental shelf. They are the most abundant species in the mesopelagic zone of the Bering Sea (Pearcy et al., 1977; Sobolevsky et al., 1996), the Gulf of Alaska (Purcell, 1996), and the eastern North Pacific Ocean off Oregon (Pearcy, 1964; Pearcy et al., 1977). Northern smoothtongue also concentrate in areas bordering the continental slope and are widely distributed from southern British Columbia to the Bering Sea (Peden, 1981) and are very abundant in the Okhotsk Sea (Sobolevsky et al., 1996).

Although larval myctophids spend day and night in nearsurface waters (Frost and McCrone, 1979), juvenile and adult northern lampfish typically inhabit depths of 300–600 m during the day (Paxton, 1967; Pearcy et al., 1977; Frost and McCrone, 1979; Sobolevsky et al., 1996; Watanabe et al., 1999). Off the Oregon coast northern lampfish exhibit semimigrant behavior: a large portion of the population migrates from a daytime depth of 300–600 m to about 50 m at night, and a nonmigratory portion of the population has both a day- and night-time vertical distribution at about 500 m depth (Pearcy et al., 1977). This semimigrant behavior also occurs in the Gulf of Alaska (Frost and McCrone, 1979), in the western North Pacific off Japan (Watanabe et al., 1999), and off California in both the San Pedro Basin (Paxton, 1967) and Santa Barbara Basin (Cailliet and Ebeling, 1990). After sunset, migratory northern lampfish have been collected at depths as shallow as 20 m in the Bering Sea (Nagasawa et al., 1997). We are unaware of any studies in which adult northern lampfish were collected at depths of less than 100 m prior to sunset.

Northern smoothtongue migrate from the mesopelagic zone (200–1000 m) in the day to the epipelagic zone (0–200 m) after sunset (Sobolevsky et al., 1996). Larval northern smoothtongue are abundant in the upper 50 m of Alaskan coastal waters during daylight (Haldorson et al., 1993; Norcross and Frandsen, 1996), but after the postlarval and early juvenile stages they are typically found at depths greater than 150 m (Taylor, 1968; Mason and Phillips, 1985). Previous accounts of adult northern smoothtongue at shallow depths were those of collections made after sunset (Barraclough, 1967; references in Hart, 1973), and in some areas adults do not exhibit diel vertical migration but remain at depths below 240 m (Mason and Phillips, 1985). There has previously been no documentation of either juvenile or adult northern smoothtongue in the upper 50 m of the water-column prior to sunset. The purpose of our study was to document the nearsurface (<15 m), daytime occurrence of both juvenile and adult northern lampfish and northern smoothtongue in Glacier Bay, Alaska.

Materials and methods

Glacier Bay is a fjord in Southeast Alaska that extends northward and bifurcates into a west arm and Muir Inlet (Fig. 1). We conducted 48 midwater trawl tows at 34 stations from 10 to 23 June 1999. Fishes were located with a Biosonics DT4000 digital 120-kHz echo sounder, and significant targets were fished with a modified herring mid-water trawl with a mouth opening of 50 m^2. Mesh sizes diminished stepwise from 5 cm in the wings to 1 cm at the codend, which was lined with 3-mm mesh. A plastic collecting bucket with 1-mm mesh was attached to the end of the codend, and was detached and rinsed after each tow. A Furuno net-sounding system monitored the depth of the headrope during fishing operations. A temperature depth recorder (TDR, Wildlife computers model MK7) was mounted on the headrope to determine the exact depth of the net during fishing oper-

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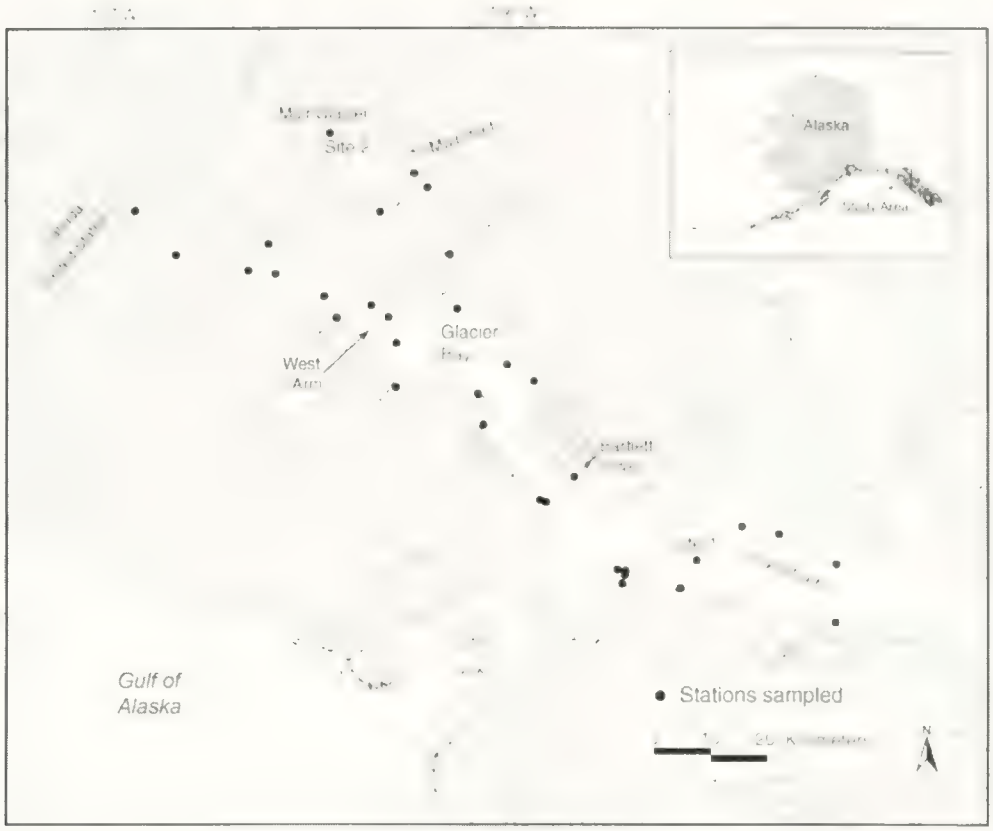

Figure 1
Stations (•) sampled by midwater trawl in Icy Strait and Glacier Bay, Alaska, during June 1999.

ations. Mid-water trawls were considered failures if the trawl doors crossed, the net mesh tore, or if the net-sounding system failed to detect the headrope of the trawl. These tows were omitted from data analysis.

We fished from a 22-m stern trawler, the RV *Pandalus*. The towing speed was about 2.5 kn, and the average tow duration was 20 minutes. There was one deep tow at site 1. At site 2 there were four tows, beginning with three shallow tows and ending with one deep tow to 100 m (Table 1). All fishing was done prior to sunset between 0839 and 1933 h ADT (Alaska daylight time). After fishing at a station, we deployed a CTD (Seabird Electronics Inc, SBE-19 SEACAT profiler) to measure water temperature (°C), salinity (ppt), density (kg/m^3), turbidity (FTU, formazine turbidity units), and chlorophyll concentration (µg/L). CTD measurements were taken every second and we present average values (n=3) of data collected in each 1-m depth interval. If multiple fishing tows were made at a station, only one CTD cast was made.

All fishes were identified in the field to the lowest possible taxon, counted, and fork length (FL) was measured to the nearest millimeter. Length-frequency histograms were plotted for northern lampfish and northern smoothtongue, and fish lengths were grouped in increments of 2 mm. Ages were estimated from length-frequency histograms based on previous studies of length-at-age and length-at-maturity for northern lampfish (Smoker and Pearcy, 1970; Nagasawa et al., 1997) and northern smoothtongue (Mason and Phillips, 1985; Sobolevsky and Sokolovskaya, 1996).

Results

Both mesopelagic species were captured infrequently; northern lampfish were present at only two of the 34 stations (n=60) and northern smoothtongue at only one station (n=133, Table 1). Northern lampfish and northern smoothtongue accounted for only 4% of the 5011 fish captured at all 34 stations; capelin (51%, *Mallotus villosus*) and walleye pollock (36%, *Theragra chalcogramma*) were the most abundant species. Northern lampfish mature at 4 years of age, and of the 60 individuals captured, about 86 % were juveniles (31–59 mm FL) and 14% were adults (65–83 mm FL). Northern smoothtongue mature at 2 years of age, and of the 133 individuals captured, about 64% were juveniles (35–53 mm FL) and 36% were adults (54–85 mm FL, Fig. 2).

At site 1, two individual northern lampfish (sizes 31 and 37 mm) were captured at 90 m depth during daylight (Fig. 1, Table 1). At site 2, next to Muir Glacier, we fished during daylight hours from 1730 to 1930 h. In the first tow (4.5 hours prior to sunset), we fished at 10–15 m depth and 12% of the northern lampfish were adults

Table 1

Station information from the two sites where northern lampfish (*Stenobrachius leucopsarus*) and northern smoothtongue (*Leuroglossus schmidti*) were present. The number of each species captured is given. Listed values of water temperature (°C), salinity (ppt), density (kg/m^3), turbidity (FTU), and chlorophyll concentration (µg/L) are those which correspond to the fishing depth.

		Site 2			
	Site 1	Tow 1	Tow 2	Tow 3	Tow 4
Northern lampfish (no.)	2	57	0	0	1
Northern smoothtongue (no.)	0	81	0	0	52
Region	Icy Strait	Muir Inlet	Muir Inlet	Muir Inlet	Muir Inlet
Date	6/12/99	6/15/99	6/15/99	6/15/99	6/15/99
Time of day	1540	1730	1830	1850	1930
Time prior to sunset (hour: min)	6:23	4:36	3:36	3:16	2:36
Latitude (North)	58° 16.28′	59° 04.27′	59° 04.13′	59° 03.95′	59° 04.44′
Longitude (West)	135° 37.38′	136° 19.93′	136° 19.07′	136° 19.07′	136° 19.59′
Bottom depth (m)	124	187	187	187	187
Fishing depth (m)	90	10-15	10	20	100
Temperature (°C)	5.77	5.18	5.69	4.83	4.28
Salinity (ppt)	32.07	30.37	29.70	30.73	31.15
Density, sigma-theta (kg/m3)	25.29	23.99	23.40	24.31	24.69
Turbidity (FTU)	8.09	14.97	15.14	14.67	11.69
Chlorophyll concentration (µg/L)	1.61	1.38	2.15	1.30	0.86

and 88% were juveniles. At 100 m (tow 4) only one northern lampfish (44 mm FL) was captured. Northern smoothtongue were also captured at depths of both 10–15 m (tow 1) and 100 m (tow 4), and both catches consisted of 39% adults and 61% juveniles.

Among all stations, oceanic parameters measured at the depth of fishing had the following ranges: temperature (4.3–8.2°C), salinity (26.3–32.1 ppt), density (20.7–25.3 kg/m^3), turbidity (7.3–15.1 FTU), and chlorophyll concentration (0.9 – 25.4 µg/L). Vertical profiles of water temperature (°C), salinity (ppt), and density (kg/m^3) at sites 1 and 2 indicated that the thermocline, halocline, and pycnocline occurred at depths <10 m. The upper 10 m of the water column at site 2 had the lowest average surface salinity (26.3 ppt) and the highest turbidity of any of the 34 stations sampled in our study. Turbidity values at site 2 were >15 FTU from 3 to 16 m and >10 FTU to depths of 41 m; turbidity at site 1 was low and ranged from 7.8 to 8.7 FTU (Fig. 3). At site 2 the maximum chlorophyll concentration (16.1 µg/L) occurred at 5 m; whereas at site 1 the chlorophyll concentration peaked (24.7 µg/L) at 12 m and remained high (>10 µg/L) to 28 m.

Discussion

Prior to sunset, juvenile and adult mesopelagic fishes were found at depths of 10 to 15 m near Muir Glacier in Glacier Bay, Alaska. Diel migrations of northern lampfish may be a response to light intensity (Paxton, 1967; Pearcy et al., 1977) or be stimulated by hunger (Pearcy et al., 1977; Cailliet and Ebeling, 1990). In the spring–summer period, when daylight hours increase in the Bering Sea, vertical migrations of northern lampfish and northern smoothtongue had smaller amplitudes and were not as distinct (Sobolevsky et al., 1996). Phytoplankton blooms and fog banks can reduce the depth to which light can penetrate, also causing northern lampfish to migrate higher in the water column (Barham, 1957).

Turbidity in the upper water layer next to Muir Glacier was higher than anywhere else in this study (15 FTU), and this high turbidity corresponded with the shallowest occurrence of mesopelagic fishes. In contrast, in Icy Strait at site 1, where the turbidity was lower, northern lampfish were captured at 90 m depth during daylight hours (Table 1, Fig. 3). High turbidity from glacial silt at Muir Glacier may significantly reduce light penetration and account for the presence of northern lampfish and northern smoothtongue at 10–15 m depth prior to actual sunset.

Although these mesopelagic fishes are more commonly distributed along the continental slope, both northern lampfish (Shimada, 1948; Taylor, 1968) and northern smoothtongue (Mason and Phillips, 1985) also occur in deep, nearshore waters from the eastern Gulf of Alaska to Puget Sound, Washington. Northern lampfish were observed in Icy Strait and Lower Glacier Bay, Alaska, previously,[1] but not as far inland as Muir Glacier. Northern smoothtongue have not been observed previously in the same area. Their occurrence along the inside waters and fjords of Southeast Alaska makes them available to a suite of predators that otherwise might feed upon them only offshore.

[1] Wing, B. 2000. Personal commun. National Marine Fisheries Service, Auke Bay Laboratory, 11305 Glacier Highway, Juneau, Alaska, 99801.

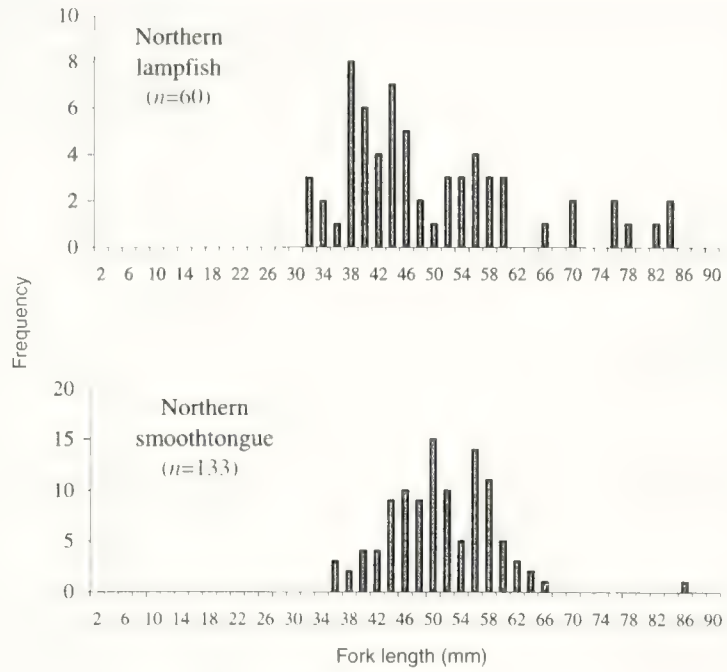

Figure 2

Length-frequency histograms for northern lampfish (*Stenobrachius leucopsarus*) and northern smoothtongue (*Leuroglossus schmidti*). Lengths were grouped in 2-mm intervals. The total number of fish that were measured is given in parentheses.

Northern lampfish and northern smoothtongue serve as important links in oceanic food webs (Cailliet and Ebeling, 1990). Myctophids provide a high-lipid energy source for a variety of predators (Van Pelt et al., 1997; Springer et al., 1999). For example, stomachs of marbled murrelets (*Brachyramphus marmoratus*) collected at the entrance to Glacier Bay contained northern lampfish almost exclusively.[2] Black-legged kittiwakes (*Rissa tridactyla*), which are restricted to foraging on fish at the surface, must feed nocturnally to obtain northern lampfish at oceanic islands in the Aleutians (Springer et al., 1996). However, near Muir Glacier and other tide-water glaciers in Glacier Bay, kittiwakes may be able to regularly forage on myctophids during daylight hours. Further investigations of fish distributions and predator diets are necessary to understand trophic interactions in Alaska's glacial fjords such as Glacier Bay.

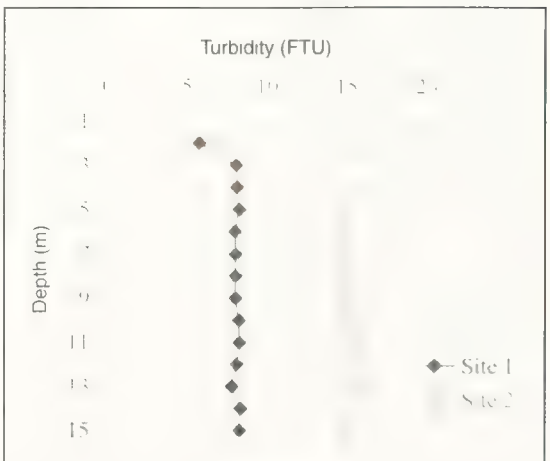

Figure 3.

Vertical profiles of turbidity (FTU, formazine turbidity units) at site 1 and site 2 from the surface to 15 m depth. Black diamonds symbolize data from site 1 and gray squares symbolize data from site 2.

Acknowledgments

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[2] Piatt, J. F. 1991. Unpubl. data. U.S. Geological Survey, 1011 E. Tudor Road, Anchorage, Alaska, 99503.

funds obtained for studies of forage fish in Glacier Bay National Park (GBNP). We thank Jim Taggart (USGS) and Mary Beth Moss (GBNP) for encouragement and logistic support.

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Opportunistic feeding of longhorn sculpin (*Myoxocephalus octodecemspinosus*): Are scallop fishery discards an important food subsidy for scavengers on Georges Bank?

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There has been much recent interest in the effects of fishing on habitat and non-target species, as well as in protecting certain areas of the seabed from these effects (e.g. Jennings and Kaiser, 1998; Benaka, 1999; Langton and Auster, 1999; Kaiser and de Groot, 2000). As part of an effort to determine the effectiveness of marine closed areas in promoting recovery of commercial species (e.g. haddock, *Melanogrammus aegelfinus*; sea scallops, *Placopecten magellanicus*; yellowtail flounder, *Limanda ferruginea*; cod, *Gadus morhua*), nontarget species, and habitat, a multidisciplinary research cruise was conducted by the Northeast Fisheries Science Center (NEFSC), National Marine Fisheries Service. The cruise was conducted in closed area II (CA-II) of the eastern portion of Georges Bank during 19–29 June 2000 (Fig. 1). The area has historically produced high landings of scallops but was closed in 1994 principally for groundfish recovery (Fogarty and Murawski, 1998). The southern portion of the area was reopened to scallop fishing from 15 June to 12 November 1999, and again from 15 June to 15 August 2000. While conducting our planned sampling, we observed scallop viscera (the noncalcareous remains from scallops that have been shucked by commercial fishermen at sea) in the stomachs of several fish species at some of these locations, namely little skate (*Raja erinacea*), winter skate (*R. ocellata*), red hake (*Urophycis chuss*), and longhorn sculpin (*Myoxocephalus octodecemspinosus*). We examined the stomach contents of a known scavenger, the longhorn sculpin, to evaluate and document the extent of this phenomenon.

Fishery discards provide food subsidies that help maintain fish populations, but to what extent is unclear. There is some evidence that fishery discards allow fish populations to be more abundant than they would be with just ambient resources (e.g. Polis and Strong, 1996). Others would counter that these discards may maintain a population but not necessarily lead to population growth (Fonds and Groenewold, 2000). As an extension of our opportunistic field observations from the closed area (CA)-II 2000 cruise, we examined NEFSC historical bottom trawl survey and food-habits databases to ascertain the role of fishery discards in the Georges Bank ecosystem, with particular respect to the longhorn sculpin population.

Materials and methods

Our sampling was conducted concurrently with the scallop fishery, therefore it was necessary to continuously monitor vessel activity in the area opened to fishing prior to our arrival and during our sampling. Prior to sampling, we collected biweekly summaries of scallop fishing vessel activity during the 1999 open season, and day by day summaries of the 2000 season were obtained from the northeast region vessel monitoring system (VMS), National Marine Fisheries Service. With this system, individual vessel locations are transmitted to NMFS every 30 minutes (McSherry[1]). The location of each fishing vessel was plotted (with Surfer 7.0; GSI, 1999) on a map overlaid with the sampling sites occupied during the 1999 study (June 1999). Stations from the 1999 study were chosen on the basis of fleet activity during the 1999 open season and our sampling goals. Each day while the RV *Albatross IV* was in CA-II, current individual scallop-vessel activity data were transmitted to us by email, plotted, and sampling stations were selected after an examination of the data.

As part of our sampling protocol, a 15-minute otter trawl haul was made at each station, towed at a speed of 6.5 km/h. A standardized NEFSC no. 36 Yankee otter trawl rigged with a rubber-disc-covered chain sweep, 11 floats, 5-m ground cables, and 450-kg polyvalent trawl doors (commonly referred to as a "flatfish net") was used. Once the trawl was on deck, we sorted fish and macro-invertebrates by species, weighed each species (0.1 kg), measured lengths of all fish (cm), examined subsamples of the fish to determine sex, maturity, and stomach contents, and collected structures to determine ages. For further details of the survey and food habits methods used in our study see Azarovitz (1981) and Link and Almeida (2000), respectively.

After initial observations of scallop viscera in fish stomachs at several previous locations, we developed an *ad hoc* study that deliberately selected two stations located in areas of high scallop fishing effort and two stations in areas of little or no scallop fishing effort. On 21–22 June 2000 we sampled stations 8B, 7D, 7E, and 8E in the northeast portion of the region open to the scallop fleet (Fig. 1). At stations 8B and 7E, we observed a high frequency of scal-

[1] McSherry, M. 1998. NMFS Northeast vessel monitoring system—operations logic and geographical display interface. NMFS NE Law Enforcement Office Internal Document, 20 p. [Available from NMFS, NEFSC, 166 Water St., Woods Hole, MA 02543.]

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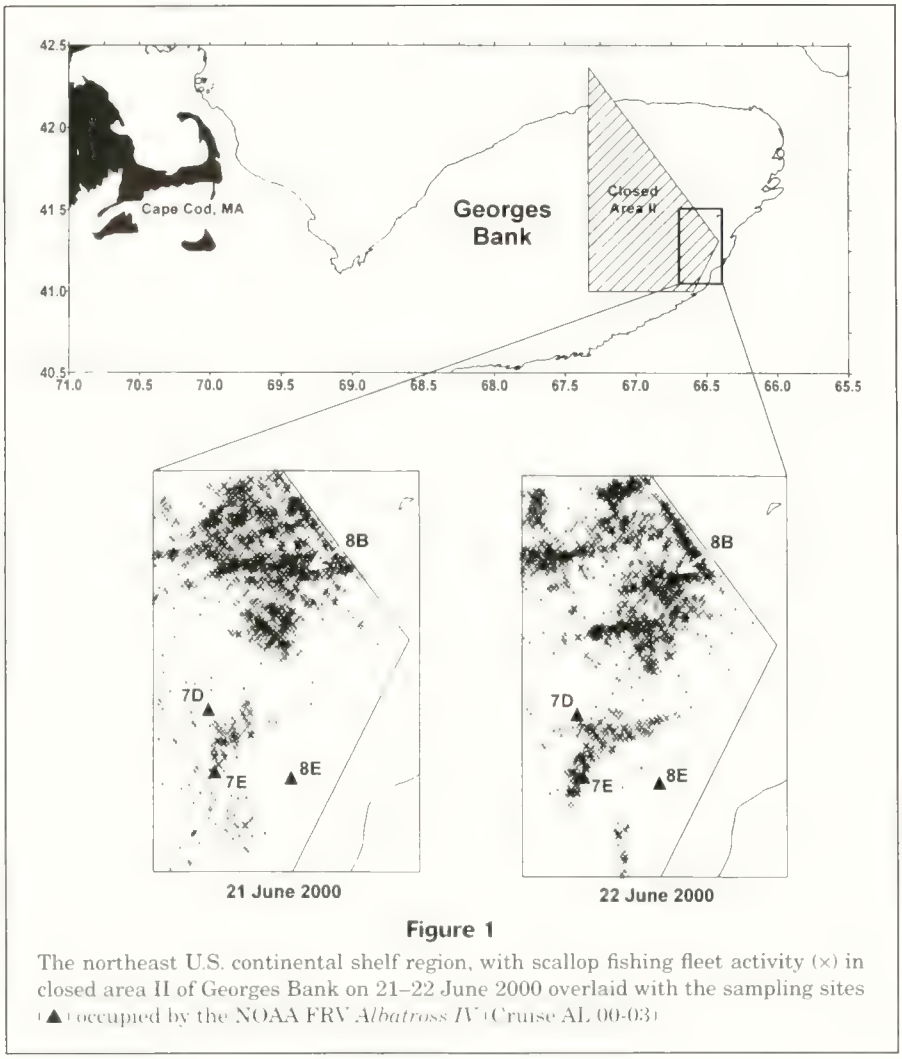

Figure 1

The northeast U.S. continental shelf region, with scallop fishing fleet activity (×) in closed area II of Georges Bank on 21–22 June 2000 overlaid with the sampling sites (▲) occupied by the NOAA FRV *Albatross IV* (Cruise AL 00-03).

lop viscera in the diets of longhorn sculpin, among other species, and undertook extra sampling of sculpin stomachs to assess the magnitude of this phenomenon. We also undertook extra sampling of sculpin at the other two stations. We present mean stomach volume and mean percent (by volume) diet composition for longhorn sculpin at these four stations.

To determine the prevalence of this phenomenon and whether discarded scallop viscera are a regular food subsidy that significantly influences the sculpin population, we examined the stratified mean number of sculpin per tow on Georges Bank (Azarovitz, 1981). We calculated this index of abundance across the fall bottom-trawl survey time series from 1963 to 1998. Additionally, we examined the mean stomach contents (cm^3), maximal stomach contents, percent frequency of occurrence of bivalve, mollusk, or pectinid viscera, and an index of gorge feeding on an annual basis from the food habits time series (Link and Almeida, 2000). The index of gorge feeding (or more simply, the gorge index) was calculated as the percent of stomachs examined with total stomach contents greater than 10 cm^3. We executed a simple linear correlation between the sculpin food-habit metrics and the index of abundance to determine if any significant relationship exists between gorge feeding and sculpin population abundance.

Results

On 21 and 22 June 2000, scallop fishing clearly occurred at stations 8B and 7E, whereas no scallop fishing occurred at 7D or 8E (Fig. 1). Rock crabs (both *Cancer irroratus* and *C. borealis*) and small crustaceans typify the diet of longhorn sculpin (Fig. 2). However, at stations in areas with scallop fishing activity, the diet of sculpin was predominately made up of scallop viscera. Crabs and small crustaceans were still a part of the diet at those stations, but did not comprise as large a percentage as was found at nondredged stations.

The volume of food in sculpin stomachs was also an order of magnitude higher at stations with intense scallop fishing activity (8B=38.7 cm^3 ±6.9; 7E=19.4 cm^3 ±12.7) than at those with no scallop fishing (8E=1.7 cm^3 ±1.4; 7D=0.3 cm^3 ±0.1). When scallop remains were present at

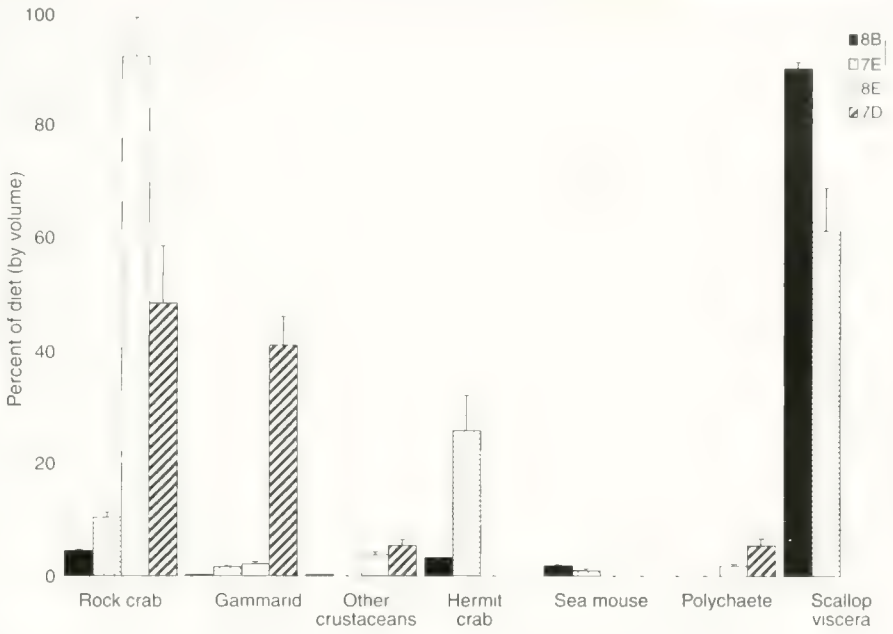

Figure 2

Diet composition (% by volume) of longhorn sculpin at two dredged and two undredged locations in closed area II. Bars are 95% confidence intervals. Sample sizes are 15, 8, 11, 6 fish at stations 8B, 7E, 8E, and 7D respectively.

a location, the amount of food consumed by sculpins increased significantly, suggesting that sculpins continued to feed on crabs and small crustaceans, but opportunistically gorged on the remains of scallops that had been shucked and thrown overboard from scallop fishing vessels operating in the region. Although anecdotal, the stomachs of all sculpins at station 8B, the station most intensely dredged, were distended beyond normal proportions for 20–25 cm fish, often extending below the pectoral fins.

The mean stomach contents of sculpin were effectively constant across the time series, averaging approximately 2 cm^3 (Fig. 3). However, the maximal stomach contents, the percent frequency of bivalve viscera, and the index of gorge feeding showed distinct patterns across the time series. All three of these metrics were generally coincident. Years with a higher gorge index corresponded to years with a high occurrence of bivalve viscera in the diet of sculpins (r=0.70, P<0.01). This finding implies that many, but not all, of the gorging events were on scallop viscera and similar discards. The highest values of the gorge index were observed in 1987 and 1998.

Longhorn sculpin abundance exhibited an initial peak and then a relatively steady period for the first 15 years of the survey, followed by a period of lower abundance during the mid-1980s and an increasing trend in the 1990s (Fig. 4). In most years sculpin abundance ranged from 10 to 20 fish per tow. The years with the highest index of sculpin abundance were 1966 and 1998. In relation to the preceding years, the index of sculpin abundance notably increased during 1966, 1987, and 1998. The latter two years correspond to years when the index of gorge feeding was highest. The correlation between the gorge index and sculpin abundance was weak (r=0.21), but significant and positive (P<0.01).

Discussion

Much of the information describing the impact of fishing gear on benthic communities and habitats has been decidedly negative. It is unclear whether populations of scavengers such as crabs, flatfish, or other demersal fish benefit from indirect effects of fishing (Kaiser and Spencer, 1994; Greenstreet and Hall, 1996; Ramsay et al., 1996) if they are not caught by the fishing gear. It is known that in the short term, scavengers, especially those small enough to fit through the mesh, are attracted to trawl and dredge tracts (e.g. Ramsay et al., 1998; Demestre et al., 2000). Additionally, some studies have actually shown that the abundance of scavenger populations increases in areas that have been trawled (reviewed in Greenstreet and Rogers, 2000). Longhorn sculpin on Georges Bank have maintained their ubiquity and abundance, albeit at relatively low levels compared with other species, during a period of intense fishing pressure in this ecosystem (Fogarty and Murawski, 1998). In recent years the sculpin population on Georges Bank has begun to increase.

Opportunistic feeding on scallop viscera appears to have a positive influence on sculpin populations. The relationship between gorge feeding and sculpin abundance is ad-

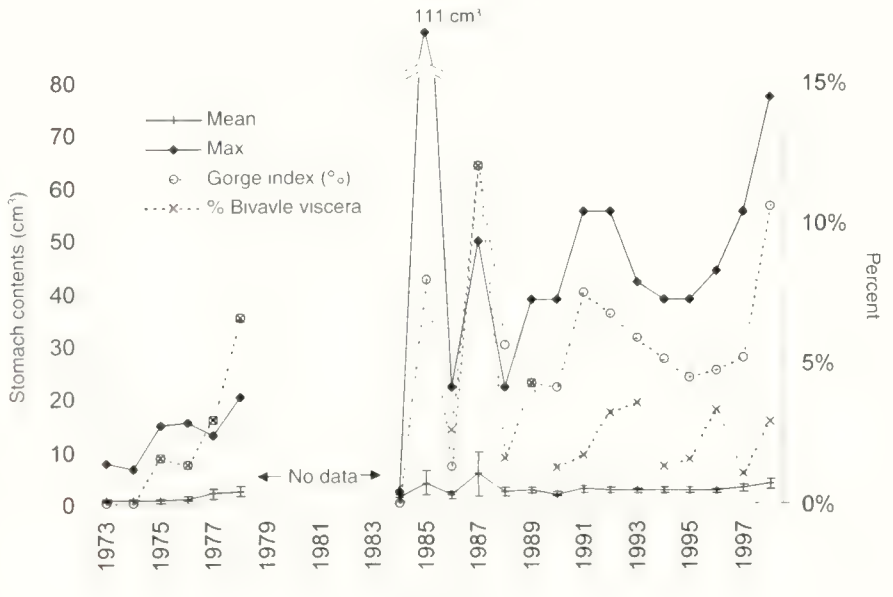

Figure 3

The mean (95% CI) and maximal (largest amount eaten) stomach contents (cm^3) of longhorn sculpin from the NEFSC food habits database. Also, the index of gorge feeding (percentage of stomachs with >10 cm^3) and percentage of stomachs containing bivalve, mollusk, or pectinid viscera.

mittedly weak, yet significant and positive. We recognize that numerous other factors could influence sculpin abundance. However we find it intriguing that the two years with the most drastic increase in sculpin abundance (in the context of recent preceding years; i.e. 1987 and 1996) occurred in years when sculpin gorge feeding was highest.

The amount of food eaten and the diet of longhorn sculpin at stations without scallop fishing activity were similar to those reported for the species on the entire northeast continental shelf (Link and Almeida, 2000) and for Georges Bank in particular (Garrison and Link, 2000). The amount of food eaten and diet at stations with scallop fishing activity showed clear evidence of gorge feeding by sculpin. Other studies have documented opportunistic feeding and changes in diet after groundfish trawling (e.g. gurnards and dabs; Kaiser and Spencer, 1994; Kaiser and Ramsay, 1997), however, this note is the first documentation of scavenging after scallop fishing. The long-term trend shows that, although the average amount of food sculpin consume is relatively constant, the composition of the diet and the frequency of gorging events varies notably. These variations may influence sculpin abundance.

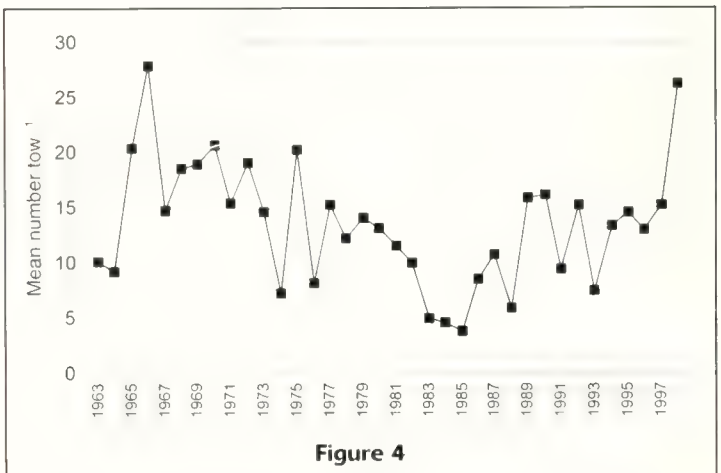

Figure 4

Index of relative abundance of longhorn sculpin from the NEFSC fall bottom trawl survey.

In the 2000 open fishing season in CA-II, more than 760 metric tons (t) of scallop meats were landed (NERO, 2000). If one conservatively assumes that scallop viscera equals the meat weight, then over 760 t (>340,000 lb) of viscera were returned to the southern part of CA-II during this two-month period. The discarded scallop viscera are a relatively small organic input, on an areal basis, to this closed area, which averages ca. 430,000 t in total annual benthic production (111 g/m^2, Cohen and Grosslein, 1987; approximately 3900 km^2 for the southern part of CA-II). How many tons of scallop viscera and similar discards have been deposited across the entire Bank over the past several decades is unknown. Yet, at a local scale scallop viscera may be an important source of energy, akin to similar processes for fish in the deep ocean (Sedberry and Musick, 1978). The biomass of scallop viscera, although

previously a part of the system, is returned in a condition much more readily available to benthic scavengers. Even weak links in terms of diet or energy can be important dynamic links in terms of population regulation (reviewed in Polis and Strong, 1996). The reintroduction of scallop viscera may not be a large addition of energy to the Georges Bank ecosystem, but it may be an important one for sculpin and other opportunist populations.

There is evidence that energy derived from fishery discards can cause scavengers to become more abundant than they would be with ambient resources (Polis and Strong, 1996), or at least these discards can help scavengers maintain population abundance under disturbed circumstances (Fonds and Groenewold, 2000). Further studies may indicate that events which produce food subsidies such as those documented in this study may be more common than generally suspected. Given the ubiquity of naval, commercial, and private vessels on the ocean, it likely that organic waste from these ships, from fishing activities, and from similar processes serves as a significant "rain of food" for benthic scavengers.

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First record of a yellowfin tuna (*Thunnus albacares*) from the stomach of a longnose lancetfish (*Alepisaurus ferox*)

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In 1987 we found a juvenile yellowfin tuna, *Thunnus albacares* (Bonnaterre, 1788), in the stomach of a longnose lancetfish, *Alepisaurus ferox* Lowe, 1833. Analysis of published information on lancetfish food habits (Haedrich, 1964, 1969; Haedrich and Nielsen, 1966; Parin, 1968; Parin et al., 1969; Fourmanoir, 1969; Grandperrin and Legand, 1970; Kubota and Uyeno, 1970; Legand et al., 1972; Kubota, 1973; Fujita and Hattori, 1976; Matthews et al., 1977) led us to conclude that this was the first record of a yellowfin tuna found in a lancetfish stomach.

Although this finding has been recorded in "gray literature" (Zamorov et al.[1]; Zamorov and Romanov[2]), the limited circulation of this type of literature, the fact that there were some inaccuracies in the details of the record, and the absence of similar findings in recent studies (Okutani and Tsukada, 1988; Moteki et al., 1993), led us to publish the finding with correct information in the following note.

Materials and methods

A juvenile yellowfin tuna (Fig. 1) in good condition was found in the stomach of a lancetfish caught by pelagic longline on 17 May 1987 during a research cruise in the waters of the exclusive economic zone of Mauritius, western Indian Ocean. The longline set position was 9°32′S, 58°03′E. The depth of hook, which caught the lancetfish, was 99 m.

Results and discussion

The fork length (FL) of the lancetfish was 167 cm, its weight was 9 kg; FL of the yellowfin tuna was 37 cm and its weight was 790 g. The tuna was immature and its stomach was empty. The tuna was 22.2% of the lancetfish body length and 8.8% of its weight. The tuna was found in the lancetfish stomach with its tail towards the mouth of the lancetfish. Evident transverse lateral damage to the tuna body included long, deep, open wounds and an absence of skin and scales in the middle part of the body. Deep wounds were absent on the head and caudal part of the tuna, where damage was minor (Fig. 2). Analysis of the photos allowed us to hypothesize about the manner of capture. Presence of transverse damage to the middle part of the body suggested that the tuna was caught by the lancetfish across the body and held until it lost its ability to swim. The teeth of the lancetfish had also caused cuts, likely inflicted during the convulsive struggle of the tuna to free itself. The absence of wounds in other parts of the tuna's body, in particular on its head, indicated that after the tuna became inactive, it was released from the predator's teeth and swallowed head-first. The proportions of the lancetfish mouth and the victim allowed the tuna to be swallowed whole.

Longnose lancetfish is a common bycatch species on tuna longlines in the study area, the northern stream of the South Equatorial Current, during the survey (April–June 1987) and are caught regularly at depths of 60–120 m. We have found slow-swimming animals in the stomachs of lancetfish (Zamorov et al.[1]; Zamorov and Romanov[2]; Romanov and Zamorov[3]). The diet of lancetfish consists of pelagic crustaceans (Hyperiidae, Portunidae, Amphipoda), cephalopods of the families Onychoteuthidae, some Ommastrephidae (*Ornithoteuthis volatilis*), Cirroteuthidae, Octopodidae, Argonautidae, Cranchiidae, Histioteuthidae, Bathyteuthidae, and mesopelagic fishes (*Sternoptyx diaphana, Paralepis elongata, Omosudis lowei, A. ferox, Antigonia rubescens, Tylerius spinosissimus*) (Haedrich and Nielsen, 1966; Parin et al., 1969; Fourmanoir, 1969; Kubota and Uyeno, 1970; Rancurel, 1970; Fujita and Hattori, 1976; Matthews et al., 1977; Moteki et al., 1993). These are slow-swimming species.[4]

[1] Zamorov V. V., A. M. Amelekhina, and A. A. Rybalko. 1992. On the feeding of *Alepisaurus ferox* Lowe, 1833 in the western Indian Ocean. *In* Fauna and ecology of animals. Proc. Zool. Mus. Odessa State Univ. 1, p. 23–37. Odessa National Univ. (ONU), 2, Dvoryanskaya St., 65000 Odessa, Ukraine. [In Russian.]

[2] Zamorov, V. V., and E. V. Romanov. 1993. New data on feeding of lancetfish *Alepisaurus ferox* Lowe, 1833. *In* Resources of tunas and related species in the World Ocean and problems of their rational utilization, p. 115–116. (Abstracts of the reports presented at first interstate conference "Resources of tunas and related species in the World Ocean and problems of their rational utilization," Kerch 1–5 June 1992). YugNIRO, Kerch. [In Russian.]

[3] Romanov, E. V., and V. V. Zamorov. 2002. Feeding habits of longnose lancetfish (*Alepisaurus ferox* Lowe, 1833) in the western Indian Ocean. Manuscript in preparation.

[4] However, small specimens of the fast-swimming ommastrephid squid *Sthenoteuthis oualaniensis* (Lesson, 1830) (mantle length <10 cm) have been found in the stomachs of lancetfish; the schooling life and common behavior of squids, including periods of slow swimming or passive drift, make them vulnerable to this predator.

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Fish. Bull. 100(2):386–389 (2002).

Figure 1

Yellowfin tuna (below) removed from the stomach of the lancetfish (above).

Figure 2

Yellowfin tuna found in lancetfish stomach; viewed from left side (**A**) and right side (**B**).

Studies show that fast-swimming animals, fishes of families Belonidae, Scombridae, Exocoetidae, Carangidae, Coryphaenidae, in particular, and most squids of the family Ommastrephidae, the ordinary food of tunas, are rare or absent in stomachs of lancetfish. Matthews et al. (1977) recorded one case of finding several frigate tunas of the genus *Auxis* in the stomach of one lancetfish, but according to Collette,[5] these were juveniles only 3.9–4.3 cm long. A small (35 cm^3 in volume) juvenile swordfish (*Xiphias gladius*) from a lancetfish stomach was reported by Williams (1967). Large slow-swimming fishes are generally found in the stomachs of lancetfish (Kubota and Uyeno, 1970, Fujita and Hattori, 1976). Cannibalism is also common among lancetfish (Haedrich, 1964; Haedrich and Nielsen, 1966; Fourmanoir, 1969; Matthews et al., 1977; Moteki et al., 1993; Zamorov et al.[1]).

[5] Collette, B. B. 1997. Personal commun. NMFS Systematic Laboratory, National Museum of Natural History, 10th & Constitution Ave. Washington DC, 20560-0153.

Large fast-swimming fish recorded from *A. ferox* stomachs include chub mackerel (*Scomber japonicus*) 35 cm long (Kubota and Uyeno, 1970) and a pink salmon (*Oncorhynchus gorbuscha*) reported by Balanov and Radchenko (1998). However, salmons (*O. gorbuscha, O. nerka,* and *O. keta*) found with slash marks attributed to lancetfish likely indicate that lancetfish also prey on these fast-swimming fish (Radchenko and Semenchenko, 1996).

The jaw structure and large teeth of lancetfish allow these fish to hunt for relatively large animals. However, large epi- and mesopelagic fishes, inhabiting the same or bordering niches with lancetfishes are able to evade attack, as a rule, because of their swimming speeds. The elongate (anguilliform) body of lancetfishes and their flabby and watery muscles suggest an inability to swim for a long time with a high cruising speed in order to chase prey. This species has no developed deep red muscles, a characteristic feature of fishes able to cruise at high speeds (Sharp and Pirages, 1978, He and Wardle, 1988). The muscle tissue of the lancetfish consists mainly of white muscles that are responsible for short-term bursts of motion (Sharp and Pirages, 1978; Schmidt-Nielsen, 1979); and its body form allows it to make short impetuous rushing movements, characteristic of many predatory fishes with anguilliform bodies (Trichiuridae, some of the Gempylidae, Muraenidae, *Anotopterus pharao*, etc.). The high dorsal fin of *A. ferox* and the large area of the caudal fin are additional signs of the high maneuverability of this species for swimming and hunting at short distances.

Yellowfin tuna, unlike lancetfish, are constantly active and swim in a rather fast motion, as has been demonstrated by numerous day-long (or several days long) telemetric tracking experiments (Carey and Olson, 1982; Cayre and Chabanne, 1986; Holland, et al., 1990; Cayre, 1991; Marsac and Cayre, 1998). To maintain hydrostatic equilibrium, small yellowfin tuna swim within the range of 1.3–1.5 body lengths per second (Brill[6]), which in the case of the tuna found in the lancetfish stomach corresponds to a rate of 48–55 cm/s. Rarely the does the speed decrease to 14–22 cm/s (Cayre and Chabanne, 1986, Holland et al., 1990, Brill et al., 1996, Marsac[7]).

Needless to say, it is not easy for a rather slow-swimming lancetfish to catch a fast-swimming tuna. In our opinion, the only way for the lancetfish to catch the tuna was to rush suddenly and to catch the prey with its large saber-like teeth. Ambush-rushing type of hunting is rather widespread among predatory fishes. Perhaps it prevails over other types of prey capture because it is efficient and requires less energetic expense than would an active chase of an escaping victim. In the pelagic environment it is hardly possible to use ambush tactics owing to the character of the pelagic environment, i.e. the absence of natural shelters. Therefore for those fish unable to use high-speed cruise swimming, the method of hunting may be that of lying motionless or slowly sneaking up on the prey and then making a violent rush to catch the prey. For the lancetfish in our study, we suggest that the tuna swam by the motionless or slowly swimming lancetfish at a distance appropriate for a rush but also close enough, so that the tuna was unable to react to or evade the attack.

Obvious lateral damage of the tuna's body may indicate that the lancetfish attacked the tuna in the vertical position either from the belly or from the back. Similar foraging behavior has been suggested for *Anotopterus pharao*, another aulopiform fish that resembles *Alepisaurus* in physical shape and structure, habitat, and diet (Balanov and Radchenko, 1998).

Several of our colleagues suggested that the tuna may have been dead when the lancetfish seized it. Starvation, or if the tunas was a discard from a fishing vessel, and other reasons were given as the cause of mortality. However, in the area of the longline set by the research cruise, and in the general vicinity of the survey, no commercial longline or tuna purse-seine vessels were spotted. We believe that the lancetfish made a successful natural attempt to seize a large, fast swimming food item. If, indeed this was the case, the finding is new and expands our knowledge of lancetfish biology. It also indicates the efficiency of ambush-rushing type of hunting and the ability of a species unable to cruise at high speeds to catch rather large fast-swimming fishes.

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Abstract—The goal of our study was to understand the spatial and temporal variation in spawning and settlement of gray snapper (*Lutjanus griseus*) along the West Florida shelf (WFS). Juvenile gray snapper were collected over two consecutive years from seagrass meadows with a benthic scrape and otter trawl. Spawning, settlement, and growth patterns were compared across three sampling regions (Panhandle, Big bend, and Southwest) by using otolith microstructure. Histology of adult gonads was also used for an independent estimate of spawning time. Daily growth increments were visible in the lapilli of snapper 11–150 mm standard length; ages ranged from 38 to 229 days and estimated average planktonic larval duration was 25 days. Estimated growth rates ranged from 0.60 to 1.02 mm/d and did not differ among the three sampling regions, but did differ across sampling years. Back-calculated fertilization dates from otoliths indicated that juveniles in the Panhandle and Big Bend were mainly summer spawned fish, whereas Southwest juveniles had winter and summer fertilization dates. Settlement occurred during summer both years and in the winter of 1997 for the southern portion of the WFS. Moon phase did not appear to be strongly correlated with fertilization or settlement. Histological samples of gonads from adults collected near the juvenile sampling areas indicated a summer spawning period.

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Temporal and spatial dynamics of spawning, settlement, and growth of gray snapper (*Lutjanus griseus*) from the West Florida shelf as determined from otolith microstructures

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A primary goal of fisheries ecology is to determine the causes of annual variation in recruitment and to predict the number of individuals that reach a harvestable size (Frank and Leggett, 1994). This variation can be substantial; recruitment to marine fish stocks can vary by one or two orders of magnitude (Shepherd and Cushing, 1990). An understanding of recruitment dynamics remains a critical, unresolved problem in fisheries science (Houde, 1987). Improved understanding is vital for better conservation of exploited marine fish populations for it would enable prediction of future harvests (Wooster and Bailey, 1987).

Gray snapper (*Lutjanus griseus*), also known as mangrove snapper, are found in the western Atlantic and Gulf of Mexico from North Carolina to Bermuda and south to Brazil. Rarely, individuals are recorded as far north as New England (Hoese and Moore, 1977). Adults generally occur offshore in areas associated with coral reefs or other hard bottom substrate. Spawning off Florida is thought to occur from June through September, and individual gray snapper probably spawn more than once during the spawning season (Starck, 1971). Larvae, which are planktonic up to about 10 mm standard length (SL) (Starck, 1971), have been reared in the laboratory and described by Richards and Saksena (1980). Juvenile gray snapper are associated with inshore *Thalassia* beds (Chester and Thayer, 1990). Young snapper remain in these *Thalassia* beds until approximately 80 mm SL when they begin to congregate around debris and channel edges. Sexual maturity occurs at 175–180 mm or three years of age (Starck, 1971).

Gray snapper support an important recreational and commercial fishery in the Gulf of Mexico. Commercial landings in the Gulf of Mexico, once over 900,000 lb in 1983 had declined to less than 430,000 lb by 1997 (Bennett[1]). Gray snapper are popular among sport fishermen; recreational landings in the Gulf of Mexico for 1997 were estimated at 877,000 lb (U.S. Dep. Commer.[2]).

The boundaries of the study area approximately represent the range of seagrass meadows along the West Florida shelf (WFS) (i.e. St. Andrew Bay is near the northwest extreme and Ft. Myers is near the southwest). The study area also experiences variation in climate, the north portion being warm-temper-

[1] Bennett, J. 1998. Automated landings assessment for responsive management. Gulf of Mexico Commercial landings for selected species, 87 p. Miami Laboratory, Southeast Fisheries Center, National Marine Fisheries Service, Miami, FL 33149.

[2] U.S. Department of Commerce. 1998. Fisheries of the United States. 1997. Current fishery statistics no. 9700, 156 p. Statistics Div, Rm 12340, 1315 East-West Highway, Silver Spring, MD 20910-3282.

ate and the southmost boundary being semitropical (Zieman and Zieman, 1989). This climate change results in latitudinal variation in the shallow water communities along the WFS: from a mainly West Indian fauna in the south to a Carolinian fauna in the north (Smith, 1976; Lyons, 1979).

The goal of our study was to improve our understanding of the recruitment dynamics of gray snapper by determining the spatial and temporal patterns in spawning and settlement along the WFS. The objectives of this study were 1) to establish spawning time through otolith back-calculation and the examination of adult gonads, 2) to determine settlement time (i.e. planktonic larval duration) from otolith microstructure, 3) to estimate growth rates for juvenile gray snapper, 4) to compare estimated spawning times, settlement times, and growth rates between sampling regions and years, and 5) to examine the potential influence of lunar phase on spawning and settlement events.

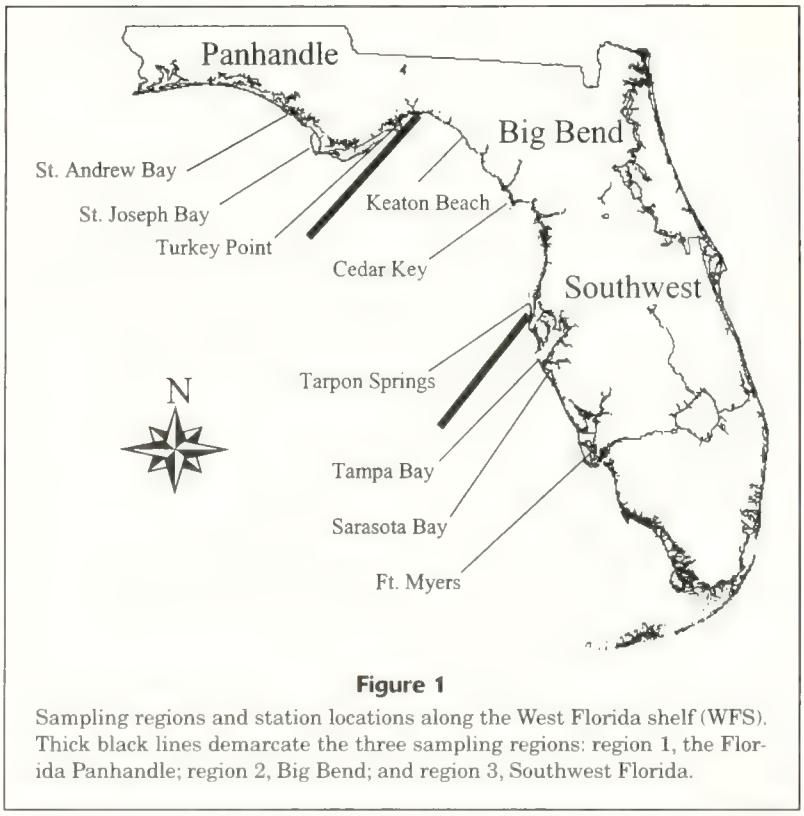

Figure 1

Sampling regions and station locations along the West Florida shelf (WFS). Thick black lines demarcate the three sampling regions: region 1, the Florida Panhandle; region 2, Big Bend; and region 3, Southwest Florida.

Materials and methods

Sampling and collection

We collected juvenile reef fish from the seagrass beds of the WFS from St. Andrew Bay in northwest Florida to Ft. Myers in southwest Florida. For spatial comparison of the results, we divided the study area into three sampling regions chosen on the basis of the differences in faunal composition (Lyons and Collard, 1974; Smith, 1976; Hoese and Moore, 1977) and type of coastal environment (Price, 1954) (Fig. 1). Region 1, the Florida Panhandle, embraces St. Andrew Bay to the St. Marks River, an area of sand beaches and barrier islands. Region 2, the Big Bend, spans the area from the St. Marks River south to Tarpon Springs. The Big Bend is unlike the other regions in that it has no barrier islands and is considered a zero-energy coastline (Murali, 1982). Region 3, Southwest Florida, includes the area from Tarpon Springs south to Ft. Myers. This region is similar to region 1 in that it is composed largely of sand beaches and barrier islands (Zieman and Zieman, 1989).

Station locations within these regions were chosen according to abundance of economically important fin fish species (Koenig and Coleman[3]). The 20 stations were located where there were large dense areas of seagrass in close proximity to the open gulf. The dominant species of seagrass in the study area is turtle-grass, *Thalassia testudinum*, followed by manatee-grass, *Syringodium filiforme*, and shoal-grass, *Halodule wrightii* (Zieman and Zieman, 1989). Station depth generally ranged from 1 to 3 meters.

We collected juvenile fish for this study every other month in 1996 and 1997, beginning in late February of 1996 and early March of 1997. At each station we made five replicate tows of 150 meters (m) in approximately 5 minutes (1.8 km/hour) using two different types of trawls. To collect the smallest postsettlement juveniles, a 1-m by 0.40-m benthic scrape constructed of a stainless steel frame with a 2-mm nylon mesh tail bag was used. This trawl was used from the beginning of the year until the fall. We used a 5-m by 3-m otter trawl with a 3-mm nylon mesh tail bag to collect larger individuals year round. The contents of each trawl were sorted and all juvenile fish of commercial value were removed, bagged, and stored on ice. At the end of a sampling trip, all juvenile fish collected were frozen. In the laboratory juvenile gray snapper were removed from samples, thawed, measured (standard length [SL] to the nearest 0.1 mm), and weighed to the nearest 0.1 g.

Otolith preparation and interpretation

Both the sagittae and lapilli were extracted from each snapper under a dissecting microscope by the "open-the-hatch method" (Secor et al., 1992). One lapillus was chosen at random from each fish for measurement. Whole lapilli were viewed with a compound microscope at 50× magnification with a video camera and monitor and the image was digitized on a microcomputer with image analysis software (BioScan, 1990). A measurement (nearest μm)

[3] Koenig, C. C., and F. C. Coleman. 1998. Recruitment indices and seagrass habitat relationships of the early juvenile stages of gag, gray snapper, and other economically important reef fishes in the eastern Gulf of Mexico. Final report (MARFIN award no. NA57FF0055) to Florida State University, 66 p. Department of Biological Sciences, The Florida State Univ., Tallahassee, FL 32306-2043.

was made from the anterior edge to the posterior edge along the longest axis.

We computed the linear regression of standard length on lapillus length to determine if otolith growth and somatic growth were proportional. To prepare lapilli for age determination, both lateral surfaces of the otolith were ground and polished on glass plates covered with a 3600- and 6000-grit polishing cloth. After being polished, the lapillus was mounted on a microscope slide with Pro-texx® mounting medium. Thirteen sagittae were also prepared to determine if sagittal section counts were consistent with lapilli counts. Because of the concave-convex shape of the sagittae, the technique used for examining the lapillus was not possible. Therefore, the more labor intensive process of embedding and sectioning the whole sagittae had to be used (Secor et al., 1992).

Growth in mm/day was estimated as the slope of the linear regression of standard length on the number of daily increments in the lapillus. Analysis of variance (ANOVA) and analysis of covariance (ANCOVA) were used to determine if estimated growth rates varied significantly among sampling regions and years.

Increment counts were made from sections of the lapilli and sagittae by using a compound microscope at 400–1000× magnification. Oil immersion was used at the 1000× magnification. Daily increments were distinguished from subdaily increments with the method of Campana (1992). Increments were counted twice by the same reader and counts that were different by no greater than 5% were averaged. Increment counts that differed by more than 5% were counted a third time, and if the third count differed by more than 5% of the previous counts, the otolith was rejected. An increment correction (3 days) was added to the total number counted based on the assumption that the first increment was not formed until after first feeding (i.e. approximately 3 days after fertilization) (Lindeman, 1997; Lindeman et al., 2000). This corrected increment count was subtracted from capture date to determine the fertilization date.

We interpreted the settlement mark in the lapillus to be where the pattern in the increment widths changed markedly (Wellington and Victor, 1989). Increments were counted from the primordium to the settlement mark and a correction of three increments was added to estimate the number of days before settlement or the planktonic larval duration. Those lapilli that did not have an obvious settlement mark were excluded from the analysis. Settlement dates were calculated by subtracting the number of post-settlement increments from the date of capture. ANOVA was used to compare the age at settlement (i.e. planktonic larval duration) with region, year, and region-year interaction. After converting lunar day of fertilization or settlement to a circular scale (Zar, 1984), we used a chi-square test to determine if fertilization and settlement dates were uniformly distributed across the lunar month.

To validate the periodicity of increment formation in lapilli we conducted an otolith marking experiment. Lapilli of live fish were marked with alizarin complexone, which has been shown to produce a well-defined mark in the otoliths of juvenile fish without producing high mortality (Tsukamoto et al., 1989; Lang and Buxton, 1993). Approximately 30 juveniles were captured with a benthic trawl and held in an 800-gallon flow-through seawater system for several days so that they might acclimate to captivity. Juveniles were fed once daily *ad libitum*. Because of the photosensitivity of alizarin complexone, juveniles were immersed in 20 L of an aerated 200 mg/L solution of alizarin complexone for 24 h in the dark. Juveniles were removed from the solution and returned to the flow-through seawater tank. Juveniles were sacrificed 7, 14, 21, or 28 days after marking and their lapilli were removed and prepared as previously described. Increments deposited after the alizarin complexone mark were counted as previously described, except that transmitted ultraviolet light was used to read increments. Linear regression was used to compare number of increments counted after the alizarin-complexone mark in the lapillus to the number of days the juveniles were held after marking. A t-test was used to determine if the slope of this regression was significantly different from 1.0.

Gonad histology and analysis

To obtain an estimate of the spawning time that was independent of otolith-based spawning dates, adult gray snapper gonads were examined. All adult gray snapper were collected as part of an ongoing study by the National Marine Fisheries Service on reef fish reproduction. Fish were collected from commercial and recreational landings from Panama City, Florida, to Ft. Myers, Florida, from January to December in 1996 and from April to November in 1997. Each fish was weighed whole (i.e. ungutted [g]) and total length (TL) and fork length were measured (mm). All fish collected were at least 252 mm TL (minimum legal size) and were assumed to be sexually mature (Domeier et al., 1996).

Gonads were removed and stored on ice and then processed by the methods of Collins et al. (1996). A small sample of each gonad was examined with a dissecting microscope (250×) to measure the maximum oocyte diameter (nearest 0.1 mm). The developmental stage of ovarian sections was determined by using the methods of Wallace and Selman (1981). Ovarian stages were assigned on the basis of the most advanced ovarian stage or follicle stage present: 1—primary growth (early oocytes); 2—cortical alveolar (previtellogenic); 3—vitellogenic; 4—hydrated; and 5—spent (i.e. presence of postovulatory follicles). Sections of testes were staged according to the methods of Moe (1969): 1—spermatogonia; 2—primary spermatocytes; 3—secondary spermatocytes; 4—spermatids; and 5—spermatozoans. The timing and duration of spawning were determined by plotting oocyte diameter and histological development stage by sampling date.

Results

Sampling and collection

Juvenile gray snapper were found in seagrass meadows along the west Florida shelf from June to November in the two most northern sampling regions, and from April

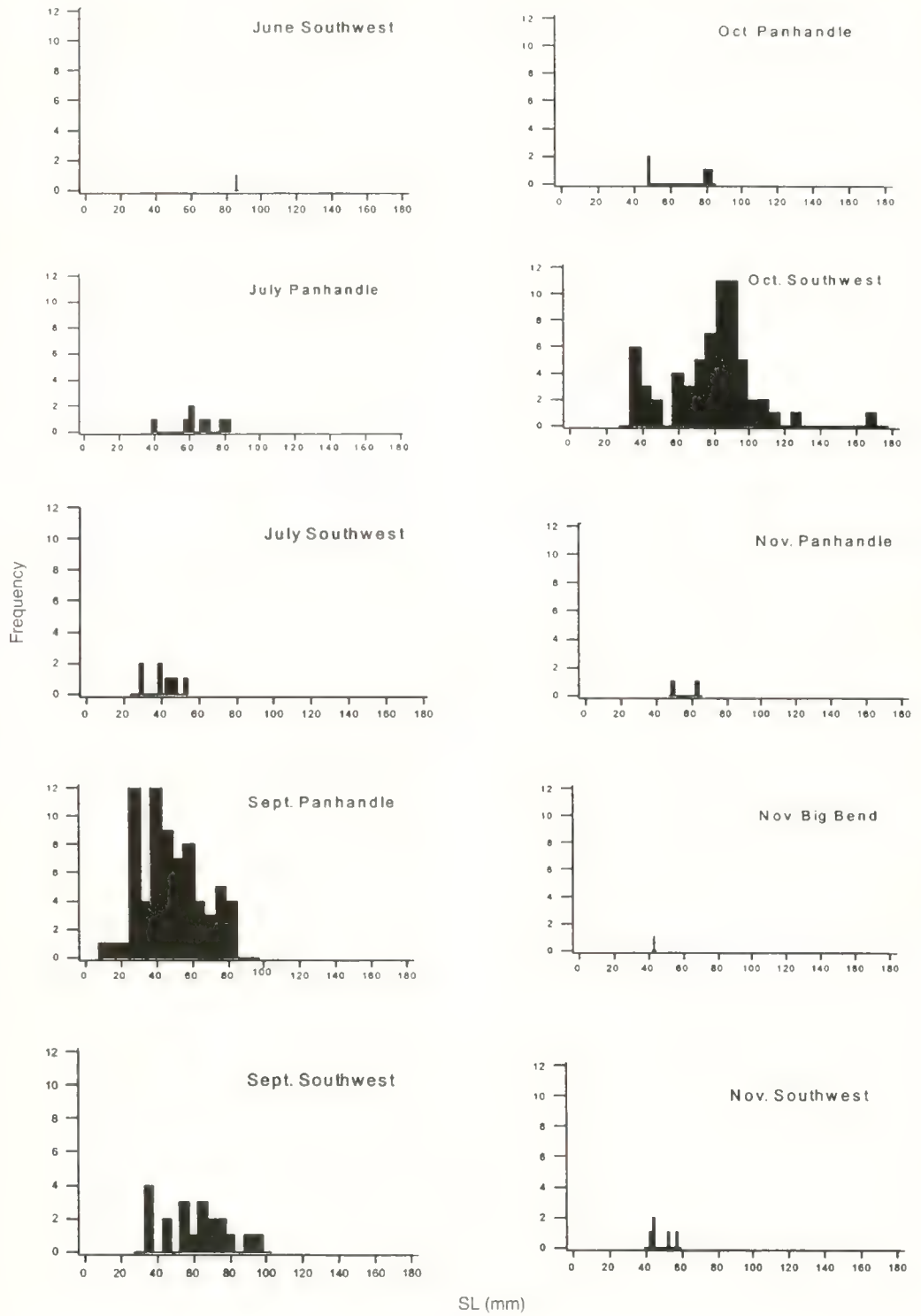

Figure 2

Length (SL, mm) frequency distribution of gray snapper juveniles by region and sampling month in 1996.

to November in the most southern area. The first juvenile was collected in the otter trawl in June 1996 from the Southwest (Fig. 2). In July we collected 14 fish in the benthic scrape and only one in the otter trawl along the entire WFS. The largest numbers were collected in September and October from the Panhandle and Southwest. The fol-

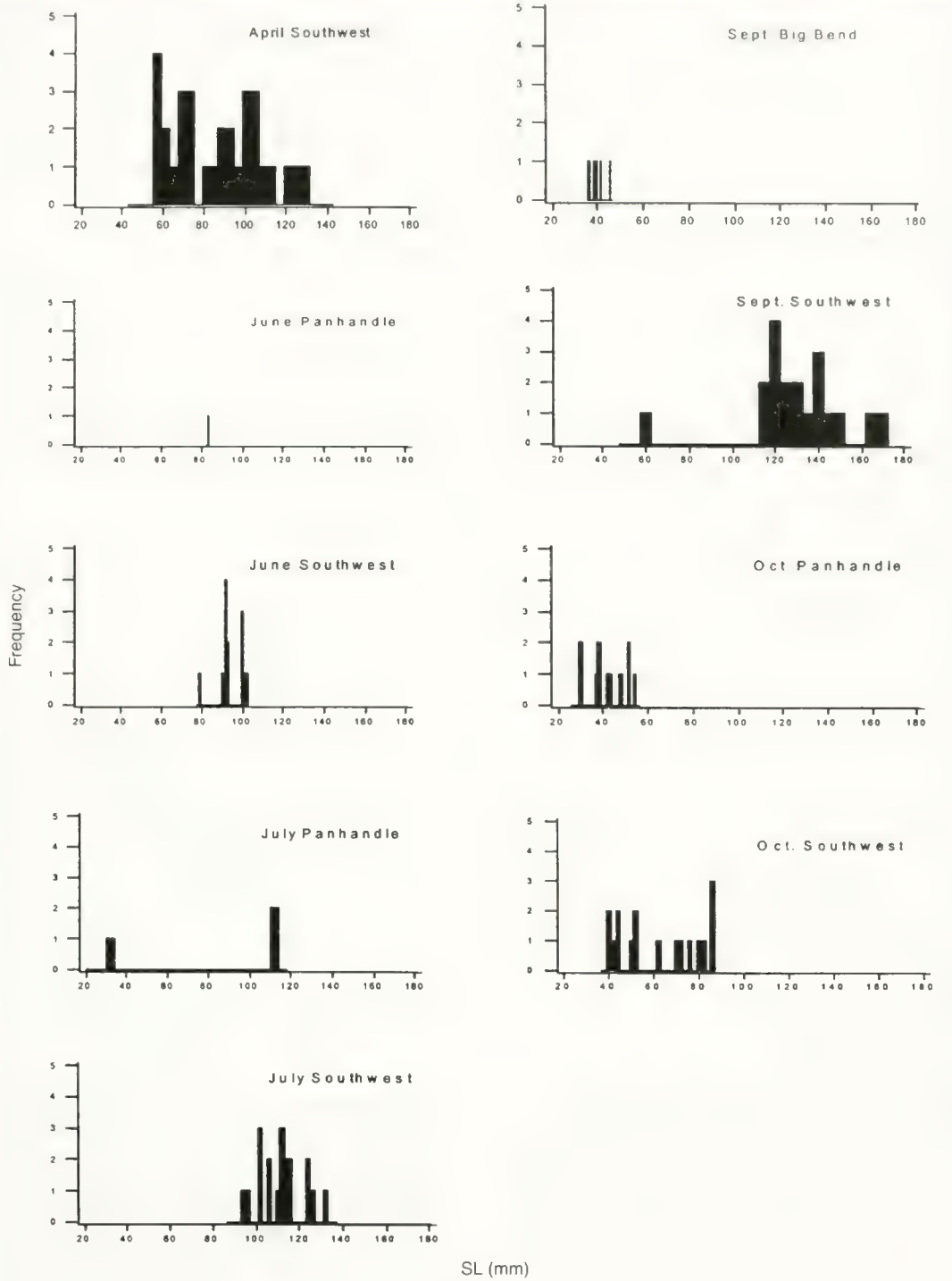

Figure 3

Length (SL, mm) frequency distribution of gray snapper juveniles by region and sampling month in 1997.

lowing year (1997), juveniles were initially collected in April in the otter trawl in the most southerly part of the Southwest sampling area (i.e. near Sanibel Island) (Fig. 3). The catch rate decreased in June, then increased during late summer, and peaked in September. Only two fish were collected in the benthic scrape, both in June.

There was evidence of multiple cohorts in the Southwest in October 1996 and in April 1997. Juveniles collected in 1997 (mean=88.3 mm SL) were, on average, about 50% larger than those collected in 1996 (mean=59.9 mm SL). Fish collected from the Southwest were also larger on average than those from the Panhandle both years.

Age and growth

Increments in the lapillus occurred at regular intervals and a consistent width and marked contrast was evident between each one. More closely spaced increments occurred at irregular intervals with less contrast between them. Usually we counted fewer increments in sagittae than in lapilli. Lapilli were thinner and flatter than sagittae and therefore required less grinding and could be examined whole, whereas sagittae had to be sectioned first. Increments near the edge of the lapilli were also clearer and easier to distinguish compared with those from sagittal sections. Increment counts were successfully assigned to 137 (71%) of the juveniles collected in 1996 and 97 (82%) of the 1997 collection. Uncorrected increment counts ranged from 35–128 (mean=75) in 1996 and 50–226 (mean=125) in 1997.

Several lines of evidence suggested that increments were deposited daily. The linear regression of SL (mm) on lapillus length (µm) indicated a highly significant relationship between body size and otolith size for fish collected in 1996 ($P<0.000$, $r^2=0.97$) and 1997 ($P<0.000$, $r^2=0.96$). Juveniles selected for the otolith marking experiment ranged from 31.4 to 44.6 mm SL (mean=38.4 mm, standard error=0.63 mm). Only 21 out of 30 surviving alizarin-complexone–marked juveniles had otoliths with visible marks and no fish harvested on day 21 had readable marks. Mean growth rate for survivors was estimated at 0.33 mm/d. The slope ($b=0.87$) of the regression of the number of increments counted after the alizarin mark on the number of days juveniles were held after marking was not significantly different from 1.0 (Fig. 4) (t-test, $P<0.05$); therefore we did not reject the hypothesis that increments were deposited daily.

Instantaneous daily growth of juvenile snapper was 1.02 mm/d in 1996 compared with 0.60 mm/d in 1997 (Fig. 5). ANOVA indicated a significant difference in slopes (i.e. growth rates) between years ($P<0.001$). However, ANCOVA indicated that there was no significant difference in growth rate among regions. Because there was a significant difference in standard lengths between years and regions, only those size ranges that overlapped between the two regions (i.e. Panhandle and Southwest, 1996: 29–83 mm SL, 1997: 39–112 mm SL) and between years (i.e. 32–110 mm SL) were included in the analysis.

Fertilization-date distribution

There were distinct patterns in the temporal and spatial distribution of fertilization dates. Our results however provided little support for lunar periodicity in spawning. Back-calculated fertilization dates indicated that surviving juveniles in the Panhandle and Big Bend were mainly summer spawned fish, whereas Southwest juveniles had winter and summer fertilization dates. In 1996, the earliest back-calculated birth date was 25 February from a fish from the Southwest, although a few (i.e. six fish) were recorded from late April and early May from the Panhandle and a few more by mid-May from the Southwest (Fig. 6). Most fish spawned beginning in mid-June and a peak in fertilization dates occurred during mid-July for both regions. Frequency of spawning then declined and the latest fertilization date of the year was recorded in mid-September from the Southwest. A chi-

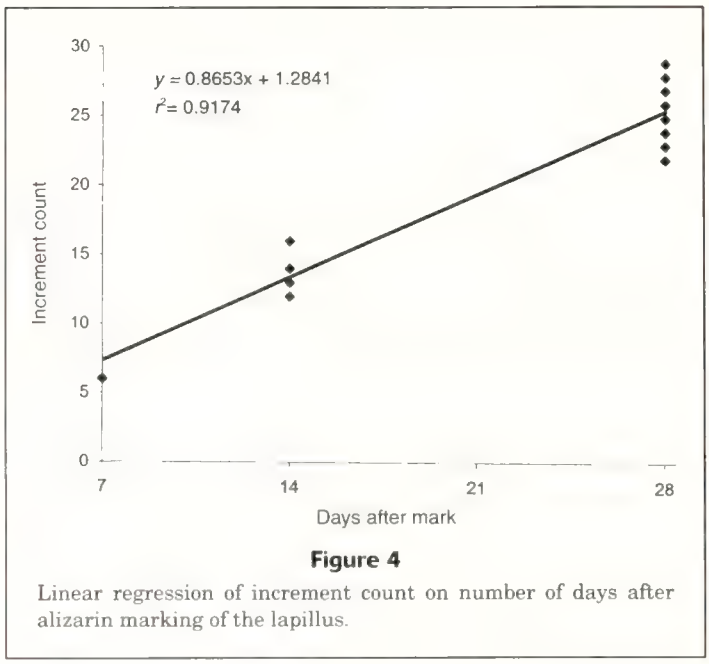

Figure 4

Linear regression of increment count on number of days after alizarin marking of the lapillus.

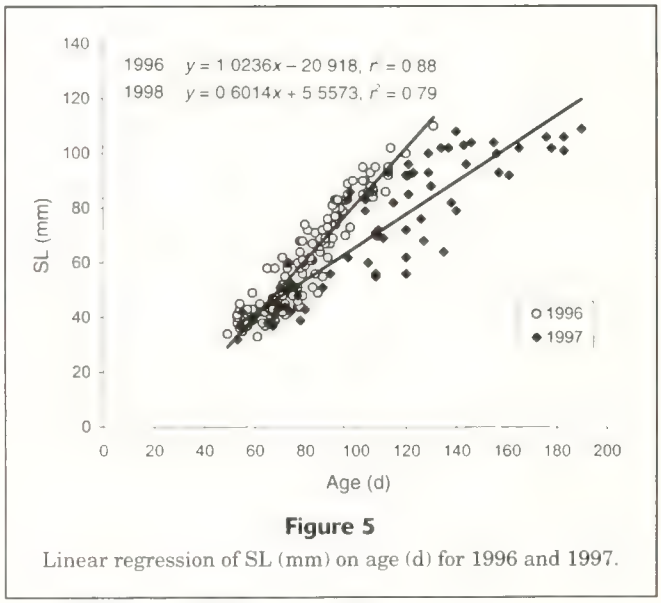

Figure 5

Linear regression of SL (mm) on age (d) for 1996 and 1997.

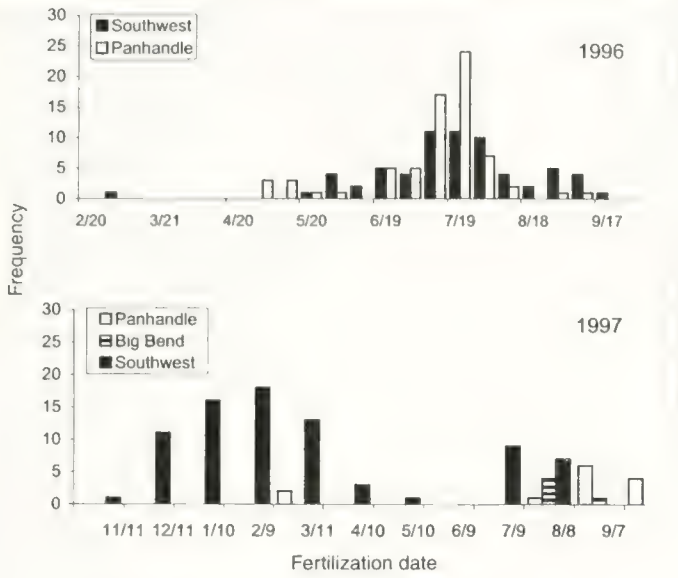

Figure 6

Fertilization-date distribution for 1996 and 1997.

square test revealed only a marginal difference ($P<0.10$) from a uniform distribution in fertilization dates across lunar month.

As in 1996, fertilization in 1997 began in mid-June, peaked in early August, and included birth dates from all three regions; however, the distribution for 1997 was bimodal. Spawning began in November of 1996 and peaked in late January of 1997, then declined into April. With the exception of two individuals collected in late February from the Panhandle, all individuals from the first fertilization-date peak were from the Southwest. The last back-calculated fertilization date for the year was in early September from the Panhandle. Fertilization dates for 1997 did not conform to a lunar cycle because a chi-square test indicated no significant difference from a uniform fertilization-date distribution across lunar month.

Results from the reproductive condition of adult gonads were compared with results from back-calculated fertilization dates from otoliths to determine if surviving juveniles were derived from a subset of the original propagules. We compared otolith data with oocyte diameters because large ova are indicative of ripe females (i.e. >0.59 mm maximum oocyte diameter) (Davis and West, 1993). In 1996, the maximum oocyte diameter distribution indicated that females were in spawning condition from May to September and that a peak in spawning activity occurred in mid-July (Fig. 7). Spawning activity, signified by the presence of hydrated oocytes, also occurred from May through mid-September. Only one female with postovulatory follicles was found in 1996, collected in mid-July. Male spawning times (i.e. May–September) mirrored those of females; however, only five males contained ripening spermatids, and none contained spermatazoa in 1996. All gonads collected in 1996 were from the Panhandle.

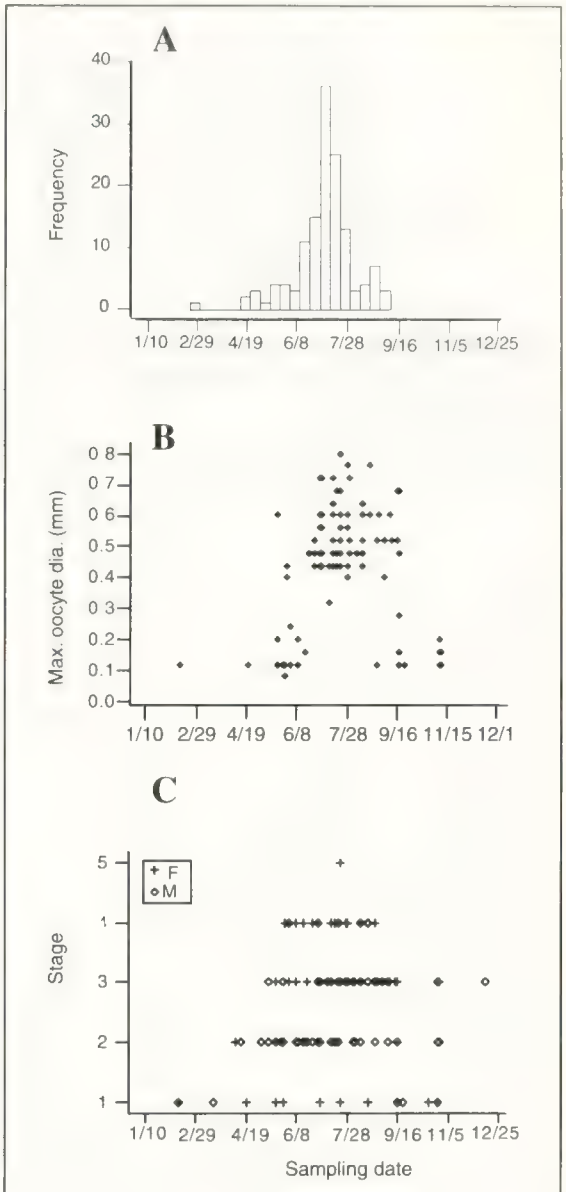

Figure 7

Comparison of spawning time as determined by back-calculation from otoliths (**A**), maximum oocyte diameter (**B**) and histological stage (**C**) for 1996. All fish were collected from the Panhandle.

In 1997 gonad data were available from all three regions and the results of comparisons of gonads from the three regions may indicate the presence of juveniles that were not derived from local spawning. Gonad data for all regions indicated peak spawning during mid-July (Fig. 8). Gonad data from the Panhandle suggested spawning times similar to those for the otolith data, i.e. a May through September spawning period and a summer peak. However, the back-calculated fertilization dates from late February and early March did not correspond to oocyte diameter or histological-stage data. Very few juveniles

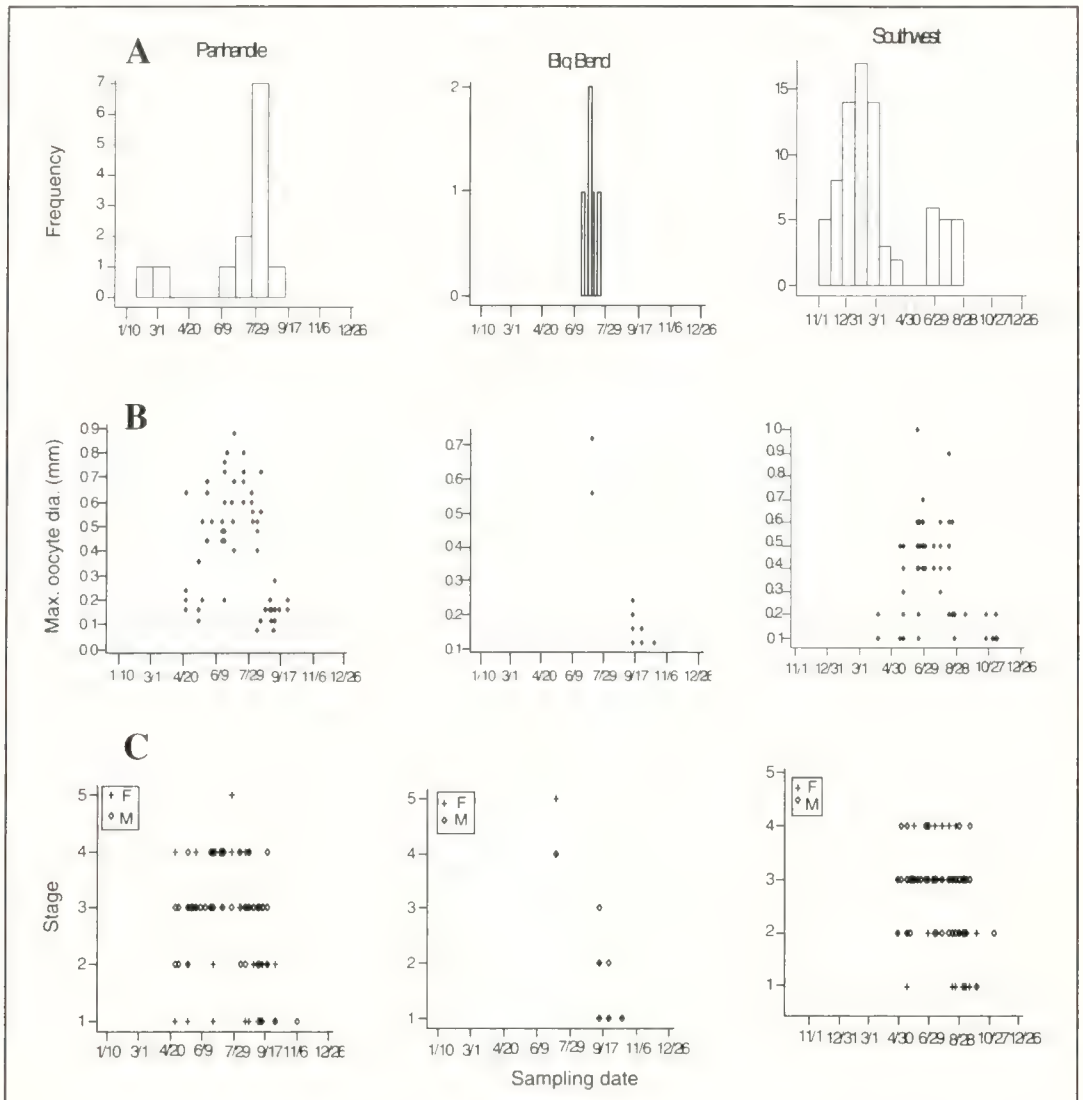

Figure 8

Comparison of spawning time as determined by back-calculation from otoliths (**A**), maximum oocyte diameter (**B**) and histological stage (**C**) for 1997.

or adult fish were collected from the Big Bend; however, these data also suggested a mid-summer spawning period. Oocyte diameter and developmental stage data from the Southwest indicated summer spawning (May to September) but because no adult gonads were collected earlier in the year, a winter fertilization-date mode (as back-calculated from otoliths) could not be determined.

Larval duration

Presumed settlement marks were distinguishable in some, but not all otoliths that were assigned ages. These marks were identified by a sharper contrast than preceding marks (Fig. 9). In addition, at this mark the increment pattern changed abruptly, postsettlement increment widths being consistently narrower than those laid down before settlement. Of the 135 otoliths collected during 1996 which were assigned ages, 80 (59%) had readily distinguishable settlement marks, whereas in 1997, 62 (64%) had distinguishable marks. The estimated age at settlement (planktonic larval duration) for 1996 and 1997 fish ranged from 20 to 32 days (mean=25 days) and from 20 to 33 days (mean=24.7 days), respectively. ANOVA indicated no significant sampling region or year effect or region-and-year interaction on the age at settlement (planktonic larval duration).

In 1996, settlement first began in mid May in the Panhandle and continued throughout the summer, peaking during the first week of August in the Panhandle and Southwest, and ending finally on 1 October in the Southwest (Fig. 10). Results for settlement date data showed no evidence for lunar periodicity in settlement, a chi-square

test indicating that the distribution of lunar settlement dates was not significantly different from a uniform distribution. The back-calculated settlement date distribution for 1997 indicated two distinct settlement events. Settlement of the first mode began in December of 1996, peaked in late winter, and then declined into late spring. All juveniles from the first event were from the Southwest. The second settlement mode was similar to that seen in the 1996 settlement date distribution, beginning in late June, peaking in early August, and finally ending in the early fall. The evidence for lunar periodicity in settlement in 1997 was weak; a chi-square test indicated only a marginally significant difference ($P<0.10$) from a uniform distribution across lunar month for 1997 settlement dates.

Figure 9
Photomicrograph (400×) of settlement mark in a lapillus of gray snapper.

Discussion

Sampling and collection

The collection of juvenile gray snapper from June to November in 1996 was consistent with a May–September spawning period found from previous studies in which the reproductive condition of adults collected off South Florida was used (Starck, 1971; Domeier et al., 1996). However, in 1997 juvenile gray snapper were initially collected in April from southwest Florida, indicating a much earlier spawning time. Differences in the timing of the first appearance of juvenile snapper for 1997 could be related to the seasonal cycle of seagrass dieback and regeneration. *Thalassia* experiences leaf die off with temperatures below 15°C (Zimmerman and Livingston, 1976). In the northern most part of the sampling region, greater leaf die off and slower growth during the spring would be expected compared with more southerly areas. This would most certainly limit the chances of survival of early settling larvae in the north because of greater predation risk and lower food availability.

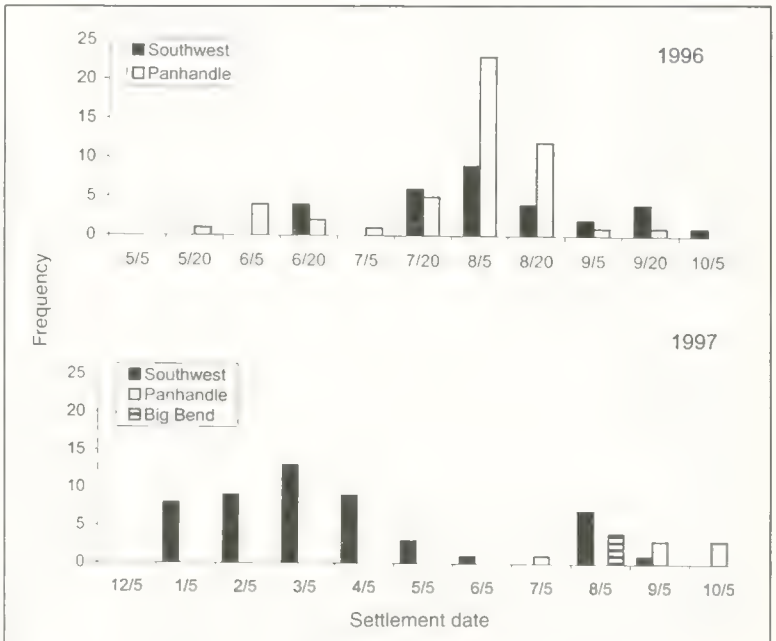

Figure 10
Settlement-date distribution for 1996 and 1997.

If gray snapper are truly recruitment-limited and if postsettlement mortality is relatively constant (Shulman and Ogden, 1987) and individuals do not migrate out of the area during the monitoring period (Robertson et al., 1988), juvenile abundance would be an effective predictor of adult abundance two to three years later when the adults are entering the fishery. Gag (*Mycteroperca microlepis*), a species with a similar early life history to that of the gray snapper, have a low rate of emigration from the seagrass nursery area during summer and a mortality rate of less than 1%/d (Koenig and Coleman, 1998). Johnson and Koenig (in press) found a strong correlation between juvenile gag abundance in seagrass meadows and year-class strength in the fishery several years later. Juvenile indices have been used successfully to document recruitment for a number of temperate fish species and invertebrates. For example, juvenile indices for striped bass were found to explain 83% of the variation in reported landings from 1963 to 1983 (Goodyear, 1985). These data for gray snapper could provide a fishery-independent method for forecasting size of year classes several years into the future. This would be a valuable addition to stock assessment which typically features age-based hind-casting methods such as

virtual population analysis from fishery-dependent data. However, before these data can be used reliably there must be a demonstrated relationship between juvenile abundance and year-class strength.

Age and growth

Because of the strong linear relationship between otolith size and fish size and the regression of increments deposited after alizarin marks on days after marking, we did not reject the hypothesis that one increment was deposited daily. In addition, Ahrenholz (2000) found no significant difference from 1 increment/d deposited from lapilli of alizarin-marked juvenile gray snapper. Juvenile congeneric red snapper (*Lutjanus campechanus*) have also been shown to deposit daily increments above a minimum growth rate (i.e. >0.3 mm/d FL) (Szedlmayer, 1998).

The daily growth rate for juveniles varied between sampling years (1 mm/d in 1996 and 0.6 mm/d in 1997) and was similar to growth rates for juvenile red snapper (0.54–0.86 mm/d, Szedlmayer and Conti, 1999). The difference in growth between years could be explained by the fact that most juveniles collected in 1997 were winter-spawned fish collected from SW Florida that may have experienced lower temperatures and that initially had a slower growth rate. Variability in the growth of larval and juvenile fish has been linked to water temperature in many species (Lang et al., 1994; Nixon and Jones, 1997). However, when the same size range of juveniles was compared between regions, there was no significant difference in growth rate. Similarly there was no difference in regional growth rate of co-occurring juvenile gag from the west Florida shelf (Fitzhugh[4]).

Fertilization-date distribution

All indicators of the temporal distribution of spawning (i.e. juvenile otoliths, oocyte diameter, and histological stage of gonads) indicated peaks in spawning from May until August and a dominant peak in mid-July. Very few gray snapper gonads were collected during the winter months in 1996 and none in 1997 because the majority of gray snapper are landed in July and August (U.S. Dep. Commer.[5]) when they aggregate on offshore reefs to spawn and are probably easier to catch (Starck, 1971; Domeier et al., 1996; Domeier and Colin, 1997). Spawning time has been related to both increasing water temperature and photoperiod for other lutjanids (Arnold et al., 1978; Grimes and Huntsman, 1980).

No obvious temporal differences were observed in reproductive development between regions from adult gonads; however, we determined winter back-calculated fertilization dates for the most southerly part of the sampling region in 1997. In contrast, Domeier et al. (1996) back-calculated spawning dates from June through September using the otoliths from juvenile gray snapper collected from south Florida. Gray snapper larvae have a relatively long pelagic stage of 25 days. The possibility exists that winter-spawned fish were produced from outside the Gulf of Mexico, perhaps from a nearby insular population, and transported from there to settle along the southwestern part of the Florida shelf. The view that winter-spawned fish were Gulf of Mexico expatriates is supported by Grimes's (1987) review of lutjanid reproduction. He found two patterns: 1) continental populations, with extended summer spawning periods; and 2) insular populations, which spawned year-round with pulses in the spring and fall. However, Domeier et al. (1996) suggested after field observations that snapper spawning patterns are species specific, as opposed to habitat dependent. We collected winter-spawned juveniles in only one of the two years of sampling; therefore it is unknown how frequently expatriate settlement events occur and what their importance to gray snapper recruitment might be.

We could not conclusively demonstrate that spawning occurs in association with lunar cycle peaks. Fertilization date hind-cast from otoliths in 1996 were only marginally associated with a lunar cycle and no relationship was evident in 1997 data. Similarly gonad stage data from adult gray snapper did not reveal any lunar pattern. However, the association of spawning with the lunar cycle has been reported for congeneric species, as well as other conspecific populations. Domeier et al. (1996) used a GSI to determine that gray snapper spawning peaked around the time of the new and full moon. Upon examination of adult gonads, Starck (1971) speculated that gray snapper spawned during or near the full moon. The congeneric species *Lutjanus vaigiensis* spawned about the time of the full moon (Randall and Brock, 1960) and *Lutjanus kasmira* spawned during both new and full moons in the laboratory (Suzuki and Hioki, 1979).

Larval duration

Presumed settlement marks were noted in many (60%) of the ageable otoliths, and they were similar in appearance to those observed for several other reef fish species (Brothers and McFarland, 1981; Victor, 1982 and 1986; Sponaugle and Cowen, 1994). Settlement marks are thought to be associated with morphological and ecophysiological changes which occur during the transition from a planktonic to a benthic life stage (Brothers and McFarland, 1981; Victor, 1982; Brothers, 1984). Several lines of evidence suggest that we correctly identified settlement marks. On average, planktonic duration, or length of the presettlement life history phase (i.e. difference between fertilization and settlement dates) was 25 days for both sampling years. Similarly, Koenig and Domeier[6] reported the planktonic

[4] Fitzhugh, G. F. 2000. Unpubl. data. National Marine Fisheries Service, 3500 Delwood Beach Road, Panama City, Florida 32408.

[5] U.S. Department of Commerce. 1998. Fisheries of the United States, 1997. Current fishery statistics no. 9700, 156 p. Statistics Division, Rm. 12340, 1315 East-West Highway, Silver Spring, MD 20910-3282.

[6] Koenig, C. C., and M. L. Domeier. 1993. Unpubl. data. Department of Biological Sciences, The Florida State Univ., Tallahassee, FL 32306-2043.

larval duration to be 24 days (21 d + 3d correction) from otoliths of wild juvenile fish collected off the Florida Keys. Richards and Saksena (1980) recorded settlement for three laboratory-reared gray snapper that were 26, 26, and 36 days old respectively. Thus, gray snapper appear to have a planktonic duration similar to the majority of reef fish (i.e. from 20 to 30 days [Victor, 1991]).

There was no obvious difference in the age at settlement among regions or years. For 1996 and 1997, the temporal distribution of settlement was about the same in the northern and southern parts of the west Florida shelf. In 1997, birth dates and corresponding settlement dates were recorded during the winter months for only the most southern sampling region. Settlement date was marginally associated with the new moon in 1997, possibly reflecting high transport into seagrass meadows at that time. Shenker et al. (1993) found a correlation between onshore transport of settlement-stage Nassau grouper (*Epinephelus striatus*) and the new moon. However, Smith (1995) found no significant association with recruitment of gray snapper through Sebastian Inlet, Florida, and lunar cycle.

Conclusions

This study established that there were differences in the timing of spawning and settlement of gray snapper across the West Florida shelf. Juveniles collected from southwest Florida indicated earlier spawning times than previously reported. Additional year-round sampling of juvenile gray snapper would help to identify the influence of early spawning events on recruitment. Further study of larval transport and genetic markers could aid in the identification of source populations.

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Current velocity and catch efficiency in sampling settlement-stage larvae of coral-reef fishes

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Abstract—Light traps and channel nets are fixed-position devices that involve active and passive sampling, respectively, in the collection of settlement-stage larvae of coral-reef fishes. We compared the abundance, taxonomic composition, and size of such larvae caught by each device deployed simultaneously near two sites that differed substantially in current velocity. Light traps were more selective taxonomically, and the two sampling devices differed significantly in the abundance but not size of taxa caught. Most importantly, light traps and channel nets differed greatly in their catch efficiency between sites: light traps were ineffective in collecting larvae at the relatively high-current site, and channel nets were less efficient in collecting larvae at the low-current site. Use of only one of these sampling methods would clearly result in biased and inaccurate estimates of the spatial variation in larval abundance among locations that differ in current velocity. When selecting a larval sampling device, one must consider not only how well a particular taxon may be represented, but also the environmental conditions under which the device will be deployed.

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With few exceptions, benthic marine organisms exhibit a complex life cycle in which larvae are dispersed pelagically and undergo a planktonic existence before they settle to the sea floor. The vagaries of dispersal by currents and unpredictable mortality of larvae in the plankton contribute to tremendous variation observed in recruitment (here defined broadly as the input of young) to adult populations. For reef fishes, the relative importance of variation in the supply of settlement-stage larvae versus postsettlement density-dependent mortality of recruits to the size and structure of local populations has been debated for some time, with evidence provided for both points of view (Doherty and Williams, 1988; Doherty, 1991; Hixon, 1991; Jones, 1991; Doherty and Fowler, 1994; Hixon and Carr, 1997; Schmitt and Holbrook, 1999). In order to determine the relative contributions of presettlement and postsettlement processes to the population dynamics of reef fishes, knowledge of spatial and temporal variation in the delivery of settlement-stage larvae to local populations is essential.

Various methods have been employed to assess the local abundance of pelagic larvae and juveniles of coral-reef fishes (Choat et al., 1993, and references therein). Two common but relatively recent sampling devices developed to sample settlement-stage reef fish larvae are light traps (Doherty 1987; Thorrold and Milicich 1990; Milicich et al. 1992; Thorrold, 1992; Meekan et al., 1993; Thorrold, 1993; Milicich and Doherty, 1994; Doherty et al., 1996; Sponaugle and Cowen, 1996a, 1996b; Thorrold and Williams, 1996; Doherty and Carleton, 1997; Sponaugle and Cowen, 1997; Leis et al., 1998; Munday et al. 1998; Meekan et al. 2000) and stationary nets, including channel nets (Shenker et al.,1993; Thorrold et al., 1994a, 1994b, 1994c) and crest nets (Dufour and Galzin, 1993; Dufour et al., 1996). Light traps are active sampling devices in that fish are attracted to, swim towards, and enter a transparent or semitransparent trap with a light source. By contrast, channel nets and crest nets passively catch larvae that are carried into them by currents or wave action, respectively. Unlike a previous study that compared light traps with towed nets (Choat et al., 1993), the goal of this study was to compare light traps and fixed-position nets, two commonly used methods for collecting settlement-stage fish larvae near coral reefs.

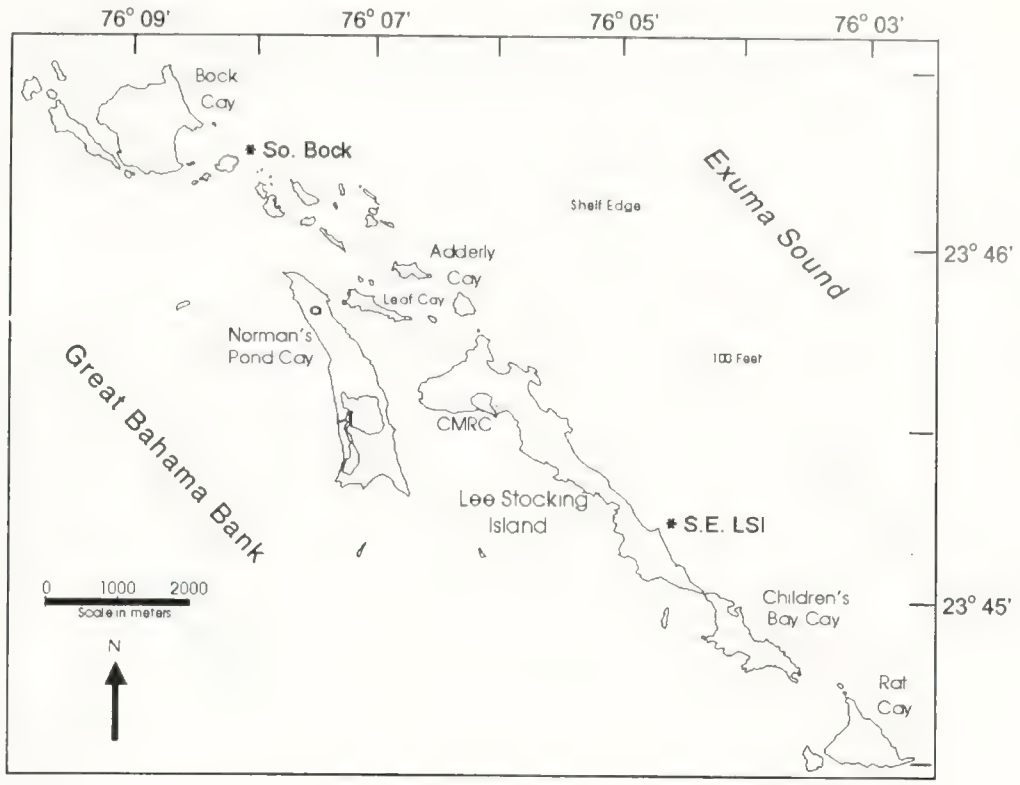

Figure 1

Location of South Bock Cay (So. Bock) and southeast Lee Stocking Island (S.E. LSI) study sites near the Caribbean Marine Research Center (CMRC), Lee Stocking Island, Bahamas.

Light traps and channel nets may not only differ in capture success for any particular species, but in the collection of larvae under varying environmental conditions such as current velocity and turbidity. Species (and the ontogenetic stages of these species) can differ in their sensitivity to light cues (Doherty, 1987; Choat et al., 1993), in swimming ability (Stobutzki and Bellwood, 1994; Leis et al., 1996; Stobutzki and Bellwood, 1997; Wolanski et al., 1997), and in the ability of larvae to interact with current velocity. For example, at relatively high current velocities, settlement-stage larvae that are photopositive but that have limited swimming speeds may not have the ability to respond to a light cue and swim into a light trap as they are carried past the sampling device. Conversely, larvae with strong swimming abilities may be able to avoid capture by channel nets at lower current velocities. Thus the relationship between the sensitivity to light cues and the ability to respond to such cues by larvae (determined by developmental stage, swimming ability, and current velocity) should determine the relative catch efficiency of these sampling devices.

Here we compare and contrast the relative number, taxonomic composition, and size of settlement-stage fish larvae caught in light traps and in channel nets deployed at two reefs that differ substantially in current velocity. Because these devices collect larvae either actively or passively, we examined 1) whether light traps are more selective and catch fewer taxa (families) than channel nets, 2) whether light traps catch larger settlement-stage larvae than channel nets, and 3) with higher current velocity, whether the relative effectiveness of light traps to channel nets decreases, resulting in fewer taxa and a lower abundance of settlement-stage larvae in light traps (with lower current velocity the opposite is true). The relative abundance and taxonomic composition of larvae caught by these two sampling devices, and how they may be modified by current velocity, might result in different interpretations concerning both magnitude and variation in larval supply.

Methods

Study sites

We conducted this study using light traps and channel nets deployed each day, from 30 July through 11 August 1997 at Lee Stocking Island (LSI), Bahamas, bracketing the new moon phase in the lunar cycle when settlement-stage fish larvae are more abundant (Thorrold et al., 1994b). Two fore-reef sites were selected *a priori* for study based upon our impression of marked differences in current velocity: South Bock Cay (So. Bock) northwest of LSI and southeast LSI (S.E. LSI), approximately 7 km south of So. Bock. So. Bock is near a channel between two cays and experiences moderate to strong tidally driven currents, whereas S.E. LSI is far from a channel where there is relatively low current velocity (Fig. 1).

Light traps

We deployed three light traps at each site on each day, from 30 July to 11 August 1997. Each of the three traps at a site was a different modification from two basic designs, with each trap rotated among stations within a site to account for any trap- or location-specific biases. One trap design had a 65-cm diameter polycarbonate top and 1.5-mm nylon mesh enclosing a volume of 200 L, with four clear plastic funnels as fish entrance holes and a fluorescent light powered by nickel-cadmium rechargeable batteries (see Sponaugle and Cowen, 1996b). A second trap design was similar but had an 80-cm diameter wood top instead of a polycarbonate top, a larger volume of 360 L, twice the number of entrance holes, a fluorescent light powered by rechargeable sealed lead-acid batteries, and an automatic timer for turning on the light remotely. The third trap design was composed of a rectangular plexiglas trap (42 cm × 38 cm × 70 cm) with rigid plexiglas panels, a plastic tray, and four entrance slots, constructed to enclose a volume of 110 L based on the design of Munday et al. (1998), but having the same electronics design as that for traps made with polycarbonate tops. All light traps were placed 3–4 m below the sea surface, suspended from moorings with subsurface buoys, and stationed approximately 12–15 m in front of each reef and 50–60 m from each other in a linear array along the offshore edge of the reef. Traps were deployed between 1730 and 1830 h and retrieved the following morning between 0900–1030. All fishes (except for ubiquitous clupeids and atherinids) were collected and placed in vials of 70% or 95% ethanol, identified to family, and later measured with vernier calipers to the nearest 0.1 mm standard length (SL).

Channel nets

We deployed one surface (0–1 m depth) and one subsurface (2–4 m depth) channel net at each site on each day (30 July to 11 August 1997) at a distance of approximately 50 m offshore of the center of the light-trap array. The channel nets were based on the design of Shenker et al. (1993), had a mesh size of 2 mm, and were positioned 30 m apart. The nets were suspended from surface buoys moored to concrete blocks or mooring anchors, allowing them to turn and fish both ebb and flood mixed-semidiurnal tides. The subsurface net mouth opening was 2 m wide × 2 m high. The mouth of each surface net was 2 m wide × 1 m high and was equipped with a General Oceanic Model 2030R2 flow meter and low-speed rotor blade suspended in the mouth opening. Flow-meter readings were recorded from the surface channel net to estimate relative current velocity between the two sites. All nets were equipped with PVC (polyvinylchloride) rods along the length of the netting to prevent entanglement during slack tides, and the codends were constructed to sink and close the end of the net to contain fish larvae during times of very low current velocity. Nets were deployed and retrieved at approximately the same time of day as the light traps. Channel nets were not sampled at dusk to distinguish catches during the day from the following night because previous studies indicated that daytime catches account for a very minor percentage of the total number of fish transported onto the Great Bahama Bank (Shenker et al., 1993; Thorrold et al., 1994c). At the laboratory, samples were rough-sorted to remove debris, fixed with 10% formaldehyde for 24–72 h, and then transferred to 70% isopropyl alcohol for later identification. Fish were measured with vernier calipers to 0.1 mm SL.

Analysis

To compare the number of taxa collected by light traps and channel nets between sites and for both sites combined, we summed the total number of families caught by each sampling device to calculate family richness. We also used the Brillouin index of species diversity (Magurran, 1988) to compare the diversity of families of fish larvae between sampling methods and sites. This index is preferable to the Shannon-Weiner index because samples collected by light traps and channel nets are nonrandom; for example, light traps produce biased samples based on the sensitivity of species to a light cue.

To compare the relative abundance of families caught by light traps and channel nets between sites and for both sites combined, we standardized catches in channel nets to the number of larvae per 1000 m^3, using flow meter readings recorded each day, and we standardized catches from light traps as the number of larvae per day. We could not standarize catches to catch per unit of effort because the length of time that the lights were operational was variable and dependent on the type of light device (see heading "Light traps") and variance in battery life. Moreover, the volume over which light traps attract larvae is difficult to quantify, especially when external factors such as current velocity may largely affect catch rates (Thorrold, 1992; Meekan et al., 2000), and Meekan et al. (2000) suggested that it is useless to convert catch rates into densities.

We used Spearman's rank correlation coefficient (Zar, 1984) to compare the relative abundance of taxa that represented at least 1% of the catch (Choat et al., 1993) for either sampling device. We also used this correlation coefficient to compare the relative abundance of taxa caught by surface and subsurface channel nets between sites for taxa that represented at least 1% of the catch for either net. In order to determine whether there were significant differences in the mean, median, and maximum length of families of fish larvae between light traps and channel nets, we used a Wilcoxon paired-sample test (Zar, 1984) in which differences in length for each family caught by both sampling devices were ranked. Finally, we used a *t*-test to test for significant differences in current velocity and the proportional abundance of total larvae caught by each sampling device between sites.

Results

Richness, diversity, relative abundance, and individual size

According to our hypotheses in regard to active and passive collection of larvae, both family richness and diversity would differ between light traps and channel nets. A total

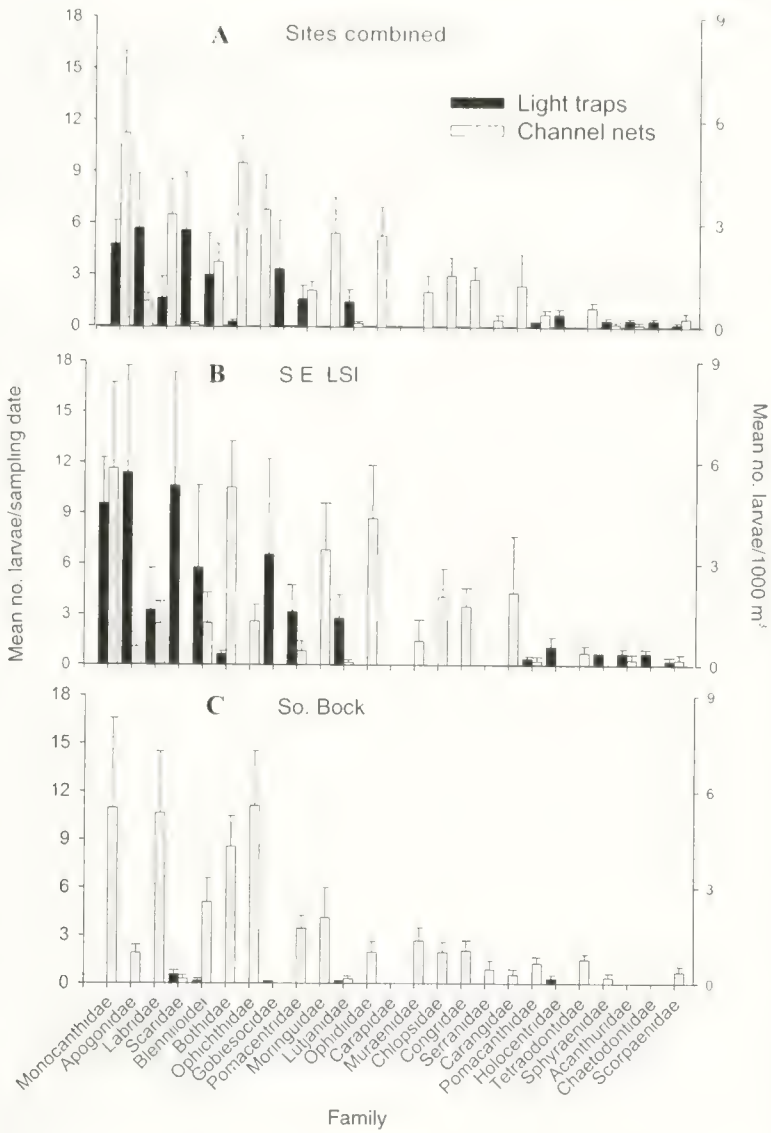

Figure 2

Abundance of 25 families of larvae that constituted at least 1% of the catch by light traps (mean no. larvae per sampling date) or channel nets (mean no. larvae per 1000 m^3) at (**A**) both study sites combined, (**B**) S.E. LSI (southeast Lee Stocking Island), and (**C**) So. Bock (South Bock Cay). Error bars are 1 SE.

of 2111 larvae were collected from light traps (n=849; 78 samples) and channel nets (n=1262; 26 surface and 26 subsurface samples), representing 20 and 33 families, respectively (Table 1), combining blenniids and labrisomids as blennioids, and not including clupeid and atherinid fishes. Synodontids were excluded from further analysis because of the presence of large postsettlement individuals in light traps. For families that constituted at least 1% of the total catch by at least one of these sampling methods, carapids, chaetodontids, gobiesocids, and holocentrids were not caught in channel nets. Conversely, carangids, chlopsids, congrids, muraenids, ophichthids, ophidiids, and tetraodontids were not represented in light-trap samples. Channel nets had higher family richness and diversity at S.E. LSI, So. Bock, and at both sites combined (Table 2) than did light traps.

There was no concordance in the rank order of abundance of families collected by light traps and channel nets at either S.E. LSI (r_s=–0.358, n=25, P>0.05), So. Bock (Spearman's rank correlation coefficient: r_s =–0.120, n=25, P>0.05), or at both sites combined (r_s=–0.162, n=25, P>0.05), including all families that represented at least 1% of the catch of either sampling device (Fig. 2). Similarly, there was no correlation in rank abundance of

Table 1

Total number of fish larvae collected from light traps and channel nets at South Bock Cay and at southeast Lee Stocking Island from 30 July to 11 August 1997. The families Blenniidae and Labrisomidae are combined as Blennioidei. Collections from surface and subsurface channel nets each day have been standardized as no. /1000 m^3. Percentage of total catch of larvae at each site for each family is denoted by (%) for light traps and for channel nets (surface and subsurface nets combined). Asterisks (*) denote families that represented at least 1% of the total catch by light traps or channel nets.

	South Bock Cay					Southeast Lee Stocking Island				
			Channel nets					Channel nets		
Family	Light traps	(%)	Surface	Subsurface	(%)	Light traps	(%)	Surface	Subsurface	(%)
Acanthuridae*						10	(1.2)	0	4.0	(0.5)
Albulidae			9.1	0	(0.9)			0	8.1	(0.9)
Antennariidae			0	1.6	(0.2)			2.4	0	(0.3)
Apogonidae*			14.1	10.7	(2.4)	148	(17.9)	10.6	3.6	(1.6)
Belonidae			1.4	0	(0.1)					
Blenniioidei*	2	(9.5)	24.1	41.8	(6.5)	75	(9.1)	27.4	5.0	(3.7)
Bothidae*			89.3	21.7	(11.0)	8	(1.0)	136.9	0	(15.6)
Callionymidae			0.8	0	(0.1)					
Carangidae*			4.1	3.0	(0.7)			56.0	0	(6.4)
Carapidae*						30	(3.6)			
Chaetodontidae*						9	(1.1)			
Chlopsidae*			24.4	0.9	(2.5)			52.8	0	(6.0)
Congridae*			25.9	0.8	(2.6)			45.4	0	(5.2)
Diodontidae								3.2	0	(0.4)
Exocoetidae			0	0.8	(0.1)					
Gobiesocidae*	1	(4.8)				85	(10.3)			
Gobiidae	2	(9.5)	0	2.4	(0.2)					
Holocentridae*	4	(19.0)				14	(1.7)			
Labridae*			17.8	120.6	(13.7)	42	(4.9)	11.6	20.1	(3.6)
Lutjanidae*	1	(4.8)	1.4	2.3	(0.4)	36	(4.4)	0	2.1	(0.2)
Microdesmidae						1	(0.1)			
Monocanthidae*			118.4	24.0	(14.1)	124	(15.0)	146.1	5.4	(17.3)
Moringuidae*			50.7	2.6	(5.3)			88.8	0	(10.2)
Muraenidae*			33.0	1.6	(3.4)			18.6	0	(2.1)
Ogcocephalidae			4.4	3.4	(0.8)			12.9	0	(1.5)
Ophichthidae*			127.3	16.9	(14.3)			32.4	1.3	(3.8)
Ophidiidae*			18.2	7.1	(2.5)			96.2	16.8	(12.9)
Pomacanthidae*			14.6	1.7	(1.6)	5	(0.6)	3.2	0	(0.4)
Pomacentridae*			35.9	8.9	(4.4)	41	(5.0)	11.0	0	(1.3)
Priacanthidae			1.4	0	(0.1)					
Scaridae*	8	(38.1)	0	3.7	(0.4)	138	(16.7)			
Scorpaenidae*			4.6	4.8	(0.9)	3	(0.4)	4.0	0	(0.5)
Serranidae*			0	11.5	(1.1)					
Sphyraenidae*			4.0	0.8	(0.5)	9	(1.1)			
Syngnathidae			4.5	0	(0.4)	1	(0.1)	18.6	0	(2.1)
Synodontidae	2	(9.5)	1.4	0	(0.1)	48	(5.8)	4.8	0	(0.5)
Tetraodontidae*			17.9	1.7	(1.9)			9.7	0	(1.1)
Unidentified	1	(4.8)	7.3	28.9	(3.6)			12.3	0	(1.4)
Total larvae	21		656.0	324.2		828		804.9	66.4	

Table 2

Richness and diversity of families of fishes caught by light traps and channel nets.

	Sites combined	South Bock Cay	Southeast Lee Stocking Island
Richness (no. families)			
Light traps	19	6	18
Channel nets	32	30	23
Diversity (Brillouin index)			
Light traps	2.845	1.179	2.832
Channel nets	3.183	3.199	3.027

subsurface and surface channel nets, including only those families that represented 1% of the catch of either net for S.E. LSI (r_s=0.227, n=16, P>0.05; Fig. 3A) or for So. Bock (r_s=0.088, n=16, P>0.05; Fig. 3B). In addition, the sizes of larvae (Table 3) caught by light traps and channel nets (but excluding families with <3 individuals collected per sampling device [acanthurids, gobiids, and syngnathids]) did not differ in the mean (sign test: n=11, P>0.05), median (n=11, P>0.05), or maximum (n=11, P>0.05) length between sampling devices. For five families that differed in length between sites and that were represented by at least three individuals (Table 3), channel nets caught significantly larger larvae at S.E. LSI than at So. Bock in mean (n=5, P=0.03) and median (n=5, P=0.03) length, but not in maximum length (n=5, P>0.05).

Current velocity and catch efficiency

Over a 10-d period in which flow-meter readings were taken simultaneously at both sites, mean daily current velocity was three-times higher at So. Bock than at S.E. LSI (t-test: t=–7.92, df=18, P=0.0001; Fig 4A). Light traps deployed at So. Bock caught on average only 3.1% of the total number of fish collected by light traps at both sites, whereas the channel nets positioned at S.E. LSI caught an average of 43.8% of the total catch for nets positioned at both sites (Fig. 4B). The mean proportional abundance of all larvae caught by light traps was significantly lower at So. Bock than at S.E. LSI (t =–50.3, df=24, P<0.0001) but there was no significant difference in proportional catch for channel nets (t=1.36, df=24, P=0.19). The difference in catch efficiency for each sampling device was also indicated by the opposite trends of abundance of taxa (apogonids, blennioids, labrids, pomacentrids, but not monocanthids) caught in at least nominally greater numbers by light traps at the low-current site (S.E. LSI) compared with the greater catch of these same taxa by channel nets at the high-current site (So. Bock). In addition, and consistent with our hypotheses concerning current velocity, light traps had higher family richness and diversity at S.E. LSI than at So. Bock, whereas the opposite was true for channel nets (Table 2).

Discussion

Differential representation of taxa between sampling methods

Light traps and channel nets differed in the taxonomic composition and the relative abundance of their catch. Expectedly, channel nets had appreciably higher family richness and diversity than did light traps, and this is consistent with our hypothesis that light traps are more selective (also see Choat et al., 1993) because not all larvae exhibit a photopositive response. One of the main differences in the relative abundance of larvae between sampling devices in the central Bahamas is that channel nets collect a large proportion of labrids and leptocephalus larvae (Shenker et al., 1993; Thorrold et al., 1994a, 1994b, 1994c; Mojica et al., 1995; this study) but light traps do not (this study). Depth-dependent distributions of larvae are also likely to contribute to differences in the relative abundance of taxa because light traps catch larvae from an unknown depth range (over which larvae are attracted to the light) whereas surface and subsurface channel nets operate at discrete depths of 0–1 m and 2–4 m, respectively. Moreover, not only can surface and subsurface channel nets differ in their catch (Fig. 3), the relative abundance of particular taxa between surface and subsurface nets can switch over time (Thorrold et al., 1994c).

The similar sizes of larvae from families caught by both light traps and channel nets are somewhat inconsistent with the findings by Choat et al. (1993), who found that larvae caught by light traps were larger than those caught by towed nets and seines. They attributed this differerence in size to a stronger photopositive response by larger pelagic larvae. The smaller size of larvae that they caught in towed nets and seines may also indicate that larger larvae may better sense the presence of these nets and avoid capture. Channel nets may decrease net avoidance by larvae because their stationary position may lessen water disturbance and hence detection of the net by incoming larvae, or possibly because other larval behaviors are exhibited.

Differential representation of taxa between sites

The greatest difference between light traps and channel nets was in their relative catch between sites. Light traps were ineffective in collecting larvae at So. Bock, whereas channel nets collected a lower but not significantly different proportion of larvae at S.E. LSI. This result cannot be explained simply by differences in the abundance of taxa between sites; the same pattern was observed for taxa sufficiently represented by both sampling devices (apogonids, blennioids, labrids, pomacentrids). These sites did differ substantially in mean current velocity, with average flow rates at So. Bock three times higher than at S.E. LSI. Shenker et al. (1993) observed that larvae collected by channel nets were significantly more abundant at a sampling station that also had greater current velocity, and this finding is consistent with our results. Similarly, Thorrold (1992) observed that light traps that were allowed to drift with water masses collected signifi-

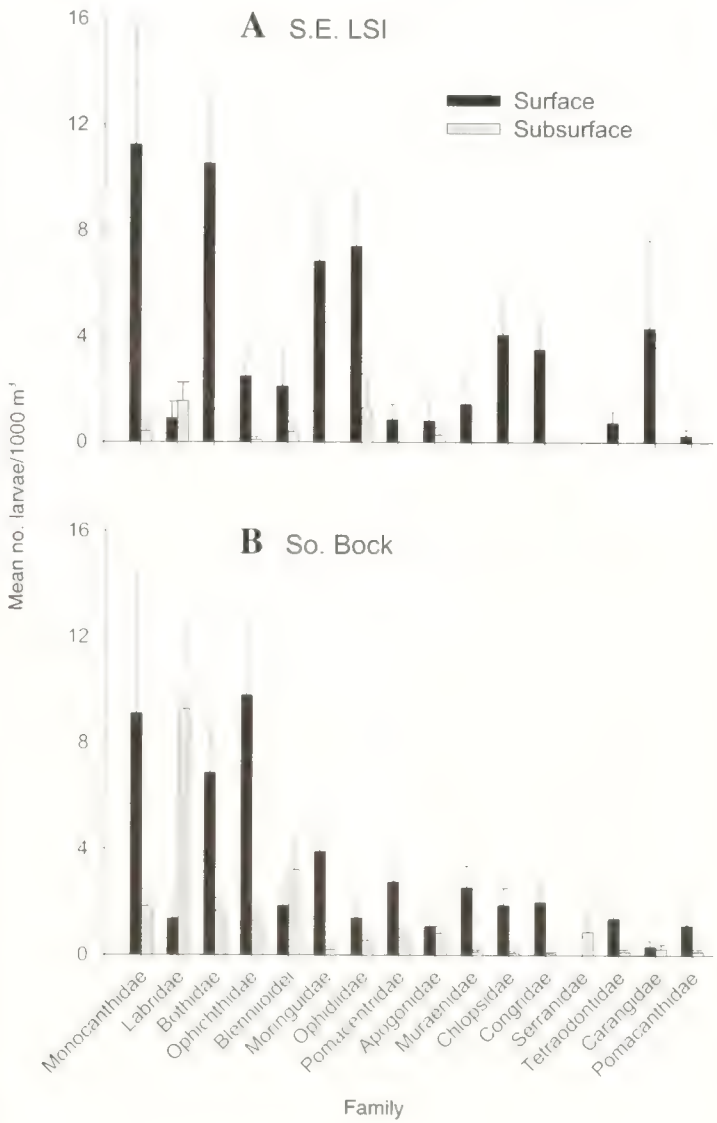

Figure 3

Abundance (mean no. larvae per 1000 m^3) of 16 families of larvae that constituted at least 1% of the catch by surface and subsurface channel nets at (**A**) S.E. LSI (southeast Lee Stocking Island), and (**B**) So. Bock (South Bock Cay). Error bars are 1 SE.

cantly more fish larvae than light traps anchored to the sea floor, apparently independent of taxa. Thorrold noted that this pattern was unexpected because more water (and presumably more larvae) should pass by anchored traps, and he suggested that the ability of larvae to swim to and enter anchored traps may be difficult under high-current conditions.

Although we conclude that between-site differences in relative catch by light traps and channel nets in our study were related to current velocity, the relationship between catch and average current velocity was not linear. The proportional abundance of larvae caught in light traps was over 31 times higher at S.E. LSI than at So. Bock, whereas the larval catch in channel nets was only 1.3 times higher at So. Bock than at S.E. LSI. The nonlinear relationship between current velocity and larval abundance may represent a threshold response in which the efficiency of light traps and channel nets may change with different current velocities. The mechanisms causing such relationships might be that fish larvae are able to orient to and swim into light traps more easily under lower current velocities, whereas fish larvae might more easily detect and avoid channel nets because of greater hydrodynamic disturbances in front of nets during higher current velocities.

Table 3

Mean (±1 SE), median, and range in size of larvae (mm standard length) collected in light traps and channel nets at South Bock Cay and at southeast Lee Stocking Island from 30 July to 11 August 1997. The families Blenniidae and Labrisomidae are combined as Blennioidei.

	South Bock Cay				Southeast Lee Stocking Island			
Family	Mean (SE)	Median	Range	*n*	Mean (SE)	Median	Range	*n*
Light traps								
Acanthuridae					25.3 (0.31)	25.2	(24.2–26.9)	9
Apogonidae					9.1 (0.12)	8.6	(6.6–14.2)	150
Blennioidei	12.6 (0.20)	12.6	(12.4–12.8)	2	11.8 (0.18)	11.6	(7.8–18.7)	83
Bothidae					13.7 (0.45)	13.5	(12.0–15.0)	7
Gobiidae	8.8 (0.10)	8.8	(8.7–8.9)	2				
Labridae					9.3 (0.29)	8.6	(6.9–12.3)	32
Lutjanidae	11.7	11.7	(11.7–11.7)	1	15.0 (0.39)	14.3	(12.6–20.8)	29
Monocanthidae					11.9 (0.19)	11.4	(7.4–21.4)	128
Pomacanthidae	13.9	13.9	(13.9–13.9)	1	9.0 (0.24)	9.1	(8.3–9.4)	4
Pomacentridae					10.9 (0.21)	10.8	(8.7–13.7)	40
Scaridae	9.1 (0.24)	8.9	(8.7–10.3)	6	8.6 (0.08)	8.7	(5.9–10.8)	120
Scorpaenidae					6.8 (0.20)	6.8	(6.4–7.1)	3
Sphyraenidae					18.0 (0.90)	18.4	(13.0–21.5)	9
Syngnathidae					40.5	40.5	(40.5–40.5)	
Channel nets								
Acanthuridae					24.7	24.7	(24.7–24.7)	1
Apogonidae	10.2 (0.24)	9.8	(8.9–14.2)	26	9.8 (0.43)	9.8	(9.0–10.5)	3
Blennioidei	12.7 (0.12)	12.7	(10.8–17.8)	65	13.6 (0.76)	12.8	(11.6–18.1)	8
Bothidae	14.8 (0.14)	14.8	(7.0–17.8)	103	16.0 (0.77)	15.1	(12.0–36.2)	29
Gobiidae	13.5 (0.24)	13.6	(13.0–13.8)	3				
Labridae	11.4 (0.06)	11.4	(9.5–13.6)	154	13.7 (1.3)	12.4	(10.9–28.7)	13
Lutjanidae	13.6 (0.38)	13.7	(12.0–14.7)	6	11.8	11.8	(11.8–11.8)	1
Monocanthidae	12.2 (0.24)	12.0	(5.2–51.3)	204	12.8 (0.29)	13.0	(7.7–18.6)	45
Pomacanthidae	8.9 (0.14)	9.0	(7.5–9.4)	12	9.2	9.2	(9.2–9.2)	1
Pomacentridae	10.2 (0.20)	9.8	(8.8–13.9)	32	12.6 (0.95)	11.8	(11.5–14.5)	3
Scaridae	9.0 (0.13)	9.0	(8.6–9.2)	4				
Scorpaenidae	8.0 (0.35)	8.1	(6.7–9.6)	9	8.1	8.1	(8.1–8.1)	1
Sphyraenidae	23.9	23.9	(23.9–23.9)	1	18.6 (3.9)	19.9	(11.3–24.6)	3
Syngnathidae	32.9 (16.9)	25.7	(7.8–65.1)	3	35.0 (1.8)	35.0	(33.2–36.8)	2

Indeed, there may be important consequences in sampling reef fish larvae among multiple sites that vary in current velocity. Current-dependent catch efficiency could confound estimates of spatial variation in larval abundance if those sites vary substantially in current velocity. For example, deploying light traps to sample larval abundance at several locations may result in higher abundances at sites with low current. This result could indicate actual larval distributions, such as accumulation of larvae on the leeward side of an island, or it could simply reflect current-dependent catch efficiency. In the latter case, estimates of larval distribution and subsequent interpretations of such distributions (e.g. larval retention) would be flawed.

As with all sampling devices, light traps and channel nets have both advantages and disadvantages for estimating larval abundance. Light traps may collect a larger proportion of settlement-stage larvae for those fishes that exhibit a photopositive response, but they catch fewer taxa and sample an unknown volume of water (Choat et al., 1993) in relation to channel nets. Our results indicate an important factor in selecting an appropriate device for estimating larval supply—namely, the hydrodynamic conditions under which the device will be deployed. Use of one sampling device, either light traps or channel nets, would have resulted in biased and potentially inaccurate relative estimates of larval abundance between So. Bock and S.E. LSI. In more recent studies, several methods have been used to estimate the abundance of as many larval fishes as possible (e.g. Leis et al., 1998), and in a comparison of light traps and towed nets in sampling freshwater fishes, Gregory and Powles (1988) concluded that both sampling devices should be used to avoid bias in the collection of larvae.

The use of both light traps and channel nets simultaneously can provide less biased estimates of spatial variation in taxonomic composition and larval supply of coral-reef fishes among sites that vary in current velocity. This com-

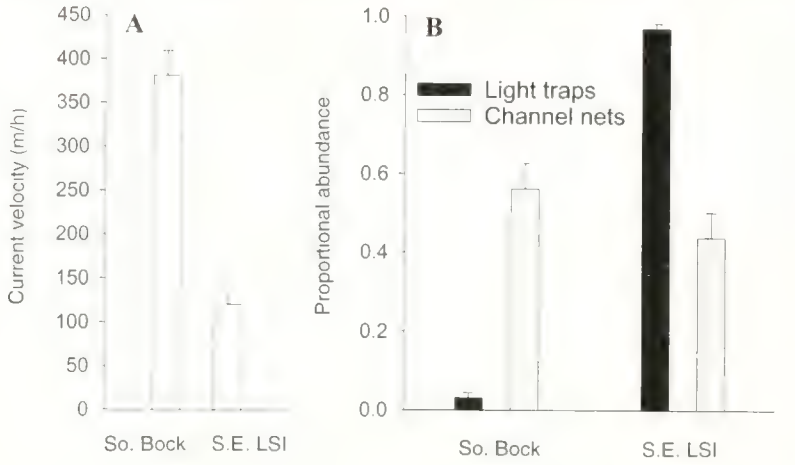

Figure 4

(**A**) Mean current velocity averaged over 24 h (m/h), and (**B**) mean daily proportional abundance of larvae caught by light traps and channel nets at So. Bock (South Bock Cay) and at S.E. LSI (southeast Lee Stocking Island). Error bars are 1 SE.

bination is problematic, however, because there is no "common currency" between light traps and channel nets. The volume of water sampled by light traps is unknown, and capture rates of larvae are very low (Meekan et al., 2000), so that the catches of light traps and channel nets cannot be easily standardized. The value of these and other larval sampling devices is that they provide a measure of temporal and spatial variation in relation to larval supply. However, the nonlinear relationship between current velocity and larval abundances observed in our study could compromise such estimates and further complicate standardization among sampling devices. Additional research is necessary to account for method-dependent differences in larval abundance among sites that differ in hydrodynamic or other environmental conditions.

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Intermingling and seasonal migrations of Greenland halibut (*Reinhardtius hippoglossoides*) populations determined from tagging studies

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Abstract—A total of 7244 Greenland halibut (*Reinhardtius hippoglossoides*, Walbaum) were tagged in Greenland waters between 1986 and 1998 to increase information on stock delineations, to clarify migration routes, and to describe the seasonal movements of fjord populations. At present 517 recaptured Greenland halibut have been recorded. For Greenland halibut released in Davis Strait, Baffin Bay, and the fjords of southwestern and eastern Greenland, a substantial portion of recovered fish demonstrated migratory behavior, up to 2500 km, primarily to Denmark Strait between Greenland and Iceland. The recaptured fish provided evidence of intermingling between the population in Denmark Strait and the populations in Davis Strait and the southwest Greenland fjords. These observations support those of other studies that indicate that Greenland halibut inhabiting Davis Strait and the fjords of southwestern and eastern Greenland originate in the spawning grounds west of Iceland. The high mobility of offshore Greenland halibut within Baffin Bay and Davis Strait suggests that Greenland halibut migrate extensively between feeding and spawning areas. Greenland halibut in the fjords of northwestern Greenland appear to be resident in behavior and do not intermingle with offshore or more southerly inshore populations. A seasonal pattern in the recovery of these fish indicates that Greenland halibut aggregate in the inner part of fjords during the second half of the year (when inshore waters are not covered with ice).

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Greenland halibut, *Reinhardtius hippoglossoides* (Walbaum), are widely distributed in the Northwest Atlantic. Their range covers a geographical area from Smith Sound, between Greenland and Canada, southward throughout Baffin Bay and Davis Strait to the northeastern coast of the United States and eastward along eastern Greenland to Iceland (Smidt, 1969; Bowering and Brodie, 1995). The spawning grounds of Greenland halibut are believed to be located southwest of Iceland (Sigurdsson[1]) and cover an extended area from Davis Strait, south of 67°N (Jensen, 1935; Smidt, 1969) to south of Flemish Pass off Newfoundland (Junquera and Zamarro, 1994) between 800 and 2000 m depths. The Greenland halibut populations off the eastern coast of Canada, in Davis Strait, in the fjords of western Greenland, in the Denmark Strait, and in Icelandic waters are believed to be recruited from these spawning grounds (Templeman, 1973; Sigurdsson[1]). A number of scientists have examined interactions among different local populations of Greenland halibut in the Northwest Atlantic. They have considered and, in some cases, attempted to quantify meristic characteristics (Templeman, 1970; Misra and Bowering, 1984; Riget et al., 1992; Rasmussen et al., 1999), genetic variability (Fairbairn, 1981; Riget et al., 1992; Vis et al., 1997), the occurrence of parasites as natural tags (Khan et al., 1982; Boje et al., 1997), and tagging data (Smidt, 1969; Bowering, 1984; Riget and Boje, 1989; Boje[2]). The results of these investigations suggest that the entire Greenland halibut population between Greenland and Canada must be considered a single stock unit. There is some evidence that the populations between Greenland and Iceland originate from a spawning stock situated along the continental slopes west of Iceland. A number of Greenland halibut populations seem to maintain a degree of isolation without any prespawning migration to their original spawning areas; this is characteristic of the Greenland halibut population in the Gulf of St. Lawrence (Khan et al., 1982) as well as for populations in the fjords of northwestern Greenland (Riget and Boje, 1989). Spawning has been observed in the Gulf of St. Lawrence (Bowering, 1980), but only a few ripe females have been sighted in the fjords of western Greenland (Riget and Boje, 1989).

Previous tagging experiments in the fjords of western Greenland (Smidt, 1969; Riget and Boje, 1989; Boje[2]) suggest that Greenland halibut stocks in the southernmost fjords may be recruited from Icelandic spawning grounds. The Irminger Current and the East Greenland Polar Current carry eggs and larvae from these spawning

[1] Sigurdsson, A. 1979. The Greenland halibut (*Reinhardtius hippoglossoides* (Walbaum)) at Iceland. Hafrannsóknir, 16, Marine Research Institute, Reykjavik, Iceland.

[2] Boje, J. 1993. Migrations of Greenland halibut in the Northwest Atlantic from tagging experiments in West Greenland 1986–89. ICES (International Council for the Exploration of the Sea) C. M. Doc. 1993/G:65, 14 p. ICES, Palægade 2-4, DK-1261 Copenhagen K, Denmark.

grounds to eastern Greenland and probably as far as southwestern Greenland (Sigurdsson[1]; Boje[3]). In 1959, Smidt (1969) observed the recapture west of Iceland of Greenland halibut that had been tagged in Licthenau Fjord in southwestern Greenland in 1954. Riget and Boje (1989) noted the recapture west of Iceland in 1980 of Greenland halibut that had been tagged in Godthaab Fjord in 1964.

In the present study, tagging experiments in the fjords of eastern and western Greenland from 1986 to 1998 are evaluated to determine the stock discreteness of Greenland halibut populations in the Northwest Atlantic and to describe seasonal migrations of Greenland halibut within inshore areas.

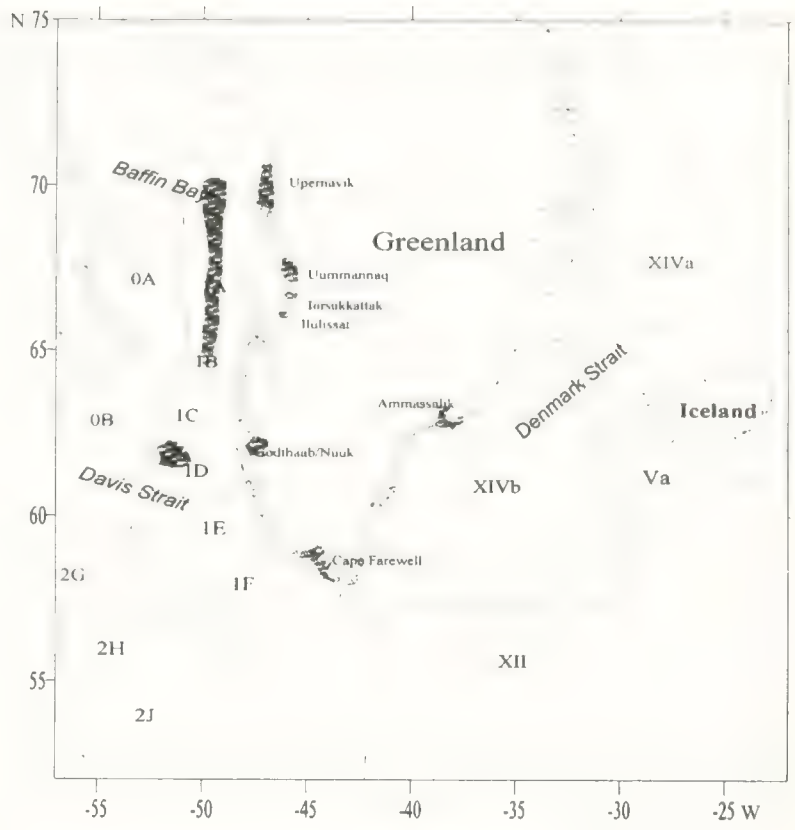

Figure 1

Map of release sites (shaded areas). NAFO (Northwest Atlantic Fisheries Organization) (0–2) and ICES (International Council for the Exploration of the Sea) (V–XIV) divisions are indicated.

Materials and methods

Greenland halibut from four areas around Greenland were tagged between 1986 and 1998. The tagging was carried out in the fjords of eastern Greenland at Ammassalik in September 1990, in the fjords of southwestern Greenland from Cape Farewell to Godthaab Fjord in January 1987–88, in the fjords of northwestern Greenland from Disko Bay to Upernavik during July–August 1986–98, and off western Greenland from Davis Strait to Baffin Bay during May–August 1991–93 (Table 1, Fig. 1). Samples were collected with longlines (Mustad Autoline Systems) from research vessels fishing at depths between 400 and 900 m—a range that is standard for the commercial fishery (Boje[4]). Fishing time for each set was approximately six hours.

A landing net was placed under each fish from the time it left the water until the fish was landed onboard the ship to avoid damage from the hook (i.e. the gravitational drag of the hook while the specimen was removed from the water). The hook was removed with care and only fish hooked in the mouth region were selected for tagging because these injuries were generally not fatal. Condition of the fish was judged visually, mainly by examining the color of the gills and by assessing internal hooking injuries. Length of the fish was measured to the nearest full centimeter (total length) and fish larger than 35 cm were selected to increase the possibility of immediate recapture in the fishery. Each fish was tagged in the musculature with a yellow T-bar tag (Floy T-bar anchor tags, FD-68B yellow) just below the dorsal fin ray near the head. Immediately after having been tagged, the fish was released.

For an evaluation of migratory routes, the numbers of recaptured fish were adjusted for fishing activities (annual landings) in recapture area (i.e. NAFO/ICES division) for the year of recapture and these numbers were expressed as the number of halibut per 100 metric tons of annual landings in the recapture division. Landing statistics were obtained from Greenland Statistical Office, NAFO Statistical Bulletin 1986–93, NAFO STATLANT 21A data and ICES Cooperative Research Reports of the ACFM 1986–98.

To analyze seasonal movements among "resident" Greenland halibut (i.e. fish caught less than 100 km from the release site) of northwestern Greenland, the fjords were stratified into five rectangles of equal area, and positioned in an east–west direction. A random-walk model (Skellam, 1951) was applied to the distribution of all releases (n=4319) pooled for the entire period, 1986–98, for all five areas, assuming equal probability that the fish would migrate either east or west or remain in the area (P=0.33). The model operated on a time unit of three months, thereby allowing each fish to move from only one rectangle to the next rectangle within a quarter of a year.

[3] Boje, J. 1997. Larval growth and spawning of Greenland halibut in West Greenland waters and the possible influences by hydrographic conditions. ICES (International Council for the Exploration of the Sea) international symposium on "Recruitment dynamics of exploited marine populations: physical-biological interactions," Baltimore 22–24 Sept. 1997. ICES, Palægade 2-4, DK-1261 Copenhagen K, Denmark.

[4] Boje, J. 1989. The fishery for Greenland halibut in Subarea 1. NAFO (Northwest Atlantic Fisheries Organization) SCR Doc. 89/27, ser. N1603, 8 p.

Table 1

Summary of numbers of tagged and recaptured Greenland halibut since 1986, comprising 517 recaptured halibut of a total of 7244 tagged fish. All fish were captured by means of longlines.

Data on tagging experiments							Information on recaptured halibut										
							Calendar years after release										
Site	Year	Month	Location	NAFO/ ICES area	Length range (cm)	Number released	0	1	2	3	4	5	6	7	8	Un-known	Total number	% of released
East Greenland fjords	1990	September	Ammassalik	XIVb	40–74	183		6	3	3	9	1		1			23	12.6
Southwest Greenland fjords	1988	January	Cape Farewell	1F	35–91	120	4	1	2	1			1				9	7.5
	1987	January	Godthaab Fjord	1D	34–110	839	14	20	9	1		1		1			46	5.5
Northwest Greenland fjords	1986	August	Ilulissat	1A	33–95	43		1	1		1						3	7.0
	1987	August	Ilulissat	1A	30–90	154	1	2	4	5	2			1			15	9.7
	1993	August	Ilulissat	1A	26–96	34											0	
	1994	August	Ilulissat	1A	34–68	71	4	2	1								7	9.9
	1986	August	Torsukkattak	1A	31–85	272	1	6	5		3	2			1		18	6.6
	1987	August	Torsukkattak	1A	38–100	384	8	21	8	10	2					3	52	13.5
	1993	August	Torsukkattak	1A	48–82	88	7	10	7								24	27.3
	1994	July	Torsukkattak	1A	36–92	144	4	14			1						19	13.2
	1996	August	Torsukkattak	1A	49–76	31	1	1									2	6.1
	1997	July	Torsukkattak	1A	44–93	264	3	15									18	6.8
	1987	August	Uummannaq	1A	36–98	244	2	7	3	8	3	3		1			27	11.1
	1993	August	Uummannaq	1A	39–87	136	3	12	6	1	2						24	17.6
	1994	August	Uummannaq	1A	42–84	49	1	2	1	1							5	10.2
	1995	August	Uummannaq	1A	41–83	363	4	25	16	4							49	14.0
	1996	August	Uummannaq	1A	39–79	574	2	21	10								33	5.7
	1998	July	Uummannaq	1A	40–80	454	13										13	2.9
	1989	August	Upernavik	1A	35–107	634	2	26	15	14	9	8	2	1			77	12.1
	1990	August	Upernavik	1A	39–106	41											0	
	1994	July	Upernavik	1A	46–92	162	4	12	5								21	13.0
	1995	July	Upernavik	1A	38–88	177	2	6	2	1							11	6.2
West Greenland offshore	1991	August	Davis Strait	1D	42–109	682	5		1	2	1			1			10	1.5
	1992	May	Davis Strait	1D	36–101	385	3	1	2			1					7	1.8
	1993	August	Baffin Bay	1A	43–92	716		1			1	2					4	0.6
Totals					26–110	7244	88	212	101	51	34	18	3	6	1	3	517	7.1

The model run covered a total of eight years, which was the maximum time recorded for time at liberty of tagged Greenland halibut at sea. The random walk distribution was compared with the true recapture distribution by means of a chi-square test. The true recapture distribution was corrected for fishing effort by using the frequency of recaptured halibut per unit landing in a statistical square (smallest statistical unit to assign landings), where landings were monthly averages for the period 1993–97. By pooling landings monthly for this 5-year period there were no zero values in the data set. Effort data were not available for the inshore fishery; therefore landings data were used instead. Previously landings data for these inshore areas were found to correlate well with fishing effort (Anonymous, 1998).

Migration distances are given in kilometers (1 km=0.540 nautical mile). For all analyses, SAS statistical (SAS, 1988) and Statistica (StatSoft, Inc., 2000) software were used.

Results

A total of 7244 Greenland halibut were tagged from 1986 to 1998. By the end of 1998, 517 recaptured Greenland halibut (7.1% of halibut released during the entire period) were recovered (Table 1). The majority of recaptured fish were reported within two years after tagging, but some were reported as late as eight years after tagging. In general, Greenland halibut tagged in the fjords of northwestern Greenland (Ilulissat, Torsukkattak, Uummannaq, and Upernavik) tended to remain resident, whereas some Greenland halibut from the three other tagging sites (East Greenland fjords, Southwest Greenland fjords, and West Greenland offshore) displayed migratory behavior.

Prevailing migratory patterns

An overview of the numbers of recaptured Greenland halibut (adjusted for fishing activity for each release site versus recapture area) is presented in Table 2. Most recaptured Greenland halibut were found at their release locality (especially at Ammassalik in East Greenland, in the fjords of Cape Farewell, in Godthaab Fjord, Uummannaq, and Upernavik in West Greenland), and 99% of the recaptured halibut were taken within the release area. For releases in the two neighboring fjords in northwestern Greenland, Ilulissat, and Torsukkattak, 10–14% of recaptured Greenland halibut showed intermingling between the two fjords. Limited intermingling was also noted between Ilulissat and Uummannaq (<1–3%). Of the 21 recaptured Greenland halibut from Davis Strait and Baffin Bay, 96% and 77%, respectively, were caught in the release area (values adjusted for fishing effort). Of 23 recaptured Greenland halibut in Ammassalik in East Greenland, the vast majority (99%) were recaptured near the tagging site; whereas single specimens (less than 1%) were recaptured in Denmark Strait and north of the Faroe Islands. Greenland halibut recovered from releases in the fjords of southwestern Greenland (Cape Farewell and Godthaab Fjord,) were mostly recaptured at the release site (99%), whereas the remaining were captured in Denmark Strait, except for a single specimen captured off Newfoundland. The majority of released halibut from the most comprehensive tagging effort in the fjords of northwestern Greenland were recaptured at their tagging site (approximately 90%). This observed fidelity to tagging site was most pronounced in the northern areas of the fjord systems at Uummannaq and Upernavik. No released fish from the fjords of northwestern Greenland were recaptured outside the area. Of the halibut released in the offshore areas of western Greenland, i.e. Davis Strait and Baffin Bay, most were recovered at their release sites, but a few specimens were also recovered as far as Denmark Strait and Newfoundland. Although only four Greenland halibut were recaptured from Baffin Bay, two of them were captured in the fjord of northwestern Greenland (Torsukkattak). Adjusted for fishing effort, they accounted for 17% of recaptured Greenland halibut from Baffin Bay.

Figure 2

Migration pattern for long-distance migrants only. Numbers indicate percentage of recaptured fish from different tagging sites in Greenland that were caught at fishing grounds shown by the arrows (northwestern Greenland Fjord Torsukkattak, off Newfoundland, west of Iceland, and north of the Faroe Islands).

Long-distance migrants

Twenty-three specimens were recovered at substantial distances from their release sites (Fig. 2). Greenland halibut tagged in Godthaab Fjord and recaptured in Denmark Strait (6 specimens) migrated an average of approximately

Table 2

Summary of data for recaptured Greenland halibut by release location and recapture area (upper numbers represent numbers adjusted for fishing effort, numbers in parentheses are percentages).

Release location	Recapture area											Total recaptured halibut (not adjusted)
	Faroe Islands	Denmark Strait	Ammassalik	Cape Farewell	Godthaab Fjord	Newfoundland	Davis Strait	Ilulissat	Torsukkattak	Upernavik	Uummannaq	
Ammassalik	2 (<1)	2 (<1)	23000 (99)									23
Cape Farewell		1 (<1)		569 (99)								9
Godthaab Fjord		1 (<1)			1459 (99)	1 (<1)						46
Davis Strait		1 (2)				1 (2)	34 (96)					17
Baffin Bay		1 (5)					17 (77)		4 (17)			4
Ilulissat								98 (83)	16 (14)		3 (3)	26
Torsukkattak								67 (10)	614 (90)			113
Uummannaq								3 (<1)			313 (99)	153
Upernavik									3 (<1)	523 (99)	4 (<1)	108
Total recaptures (not adjusted)	1	17	16	7	39	3	14	42	100	105	155	499[1]

[1] Only 499 fish of 517 fish total recaptured had reliable information on recapture position.

1100 km: whereas fish released in Godthaab Fjord and Davis Strait and recaptured off Newfoundland (1 and 2, respectively) migrated an average of 1800 km. A single fish recaptured north of the Faroe Islands was released at Ammassalik in eastern Greenland. All recaptured Greenland halibut in Denmark Strait had been released at inshore areas of eastern and southern Greenland or from offshore areas of western Greenland. From the latter area, one fish tagged in Baffin Bay had thus migrated about 2500 km. Recaptured Greenland halibut off Newfoundland were tagged in Davis Strait and Godthaab Fjord. Two fish released from Baffin Bay were recaptured in the northern fjord of Disko Bay (Torsukkattak).

A cumulative distribution of estimated migration distance for each main release site (Fig. 3) revealed that Greenland halibut from the offshore area of western Greenland were the more frequent long-distance migrants, and only about 50% were resident. About 70% of recaptured Greenland halibut from East Greenland fjords migrated 400 km or less. Approximately 80% of Greenland halibut from the fjords of southwestern Greenland were resident, whereas the remaining 20% undertook migrations of 1000–1200 km. Nearly all Greenland halibut in the northwestern fjords were resident and migrated less than 100 km.

Inshore seasonal migration

Recapture data from the fjords of northwestern Greenland were examined to determine whether recapture location varied seasonally, i.e. whether seasonal migrations occurred. The inshore fishery is carried out in all seasons mainly with longlines. Catches tend to peak during the warmer period in July–August, when water is free from ice in the inner part of the fjords, but substantial numbers are also caught from January to June, when waters are covered by ice, in a fishery distributed throughout

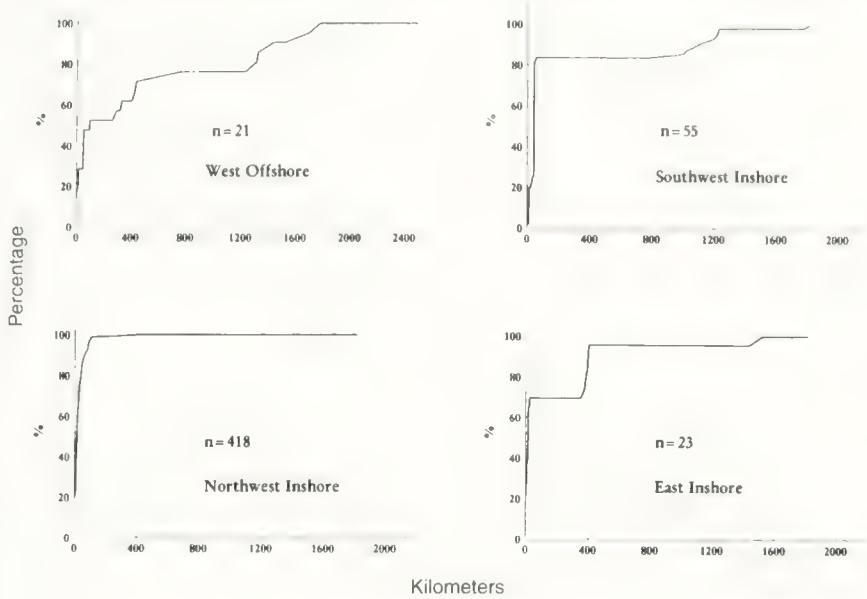

Figure 3

Cumulative distribution of distance (km) migrated by released Greenland halibut from four main areas. *n* = number of recaptured fish.

the fjord (Simonsen and Boje[5]). The catch-adjusted recapture data were categorized by stratifying the fjords into five rectangles of equal area, ranging from the mouth of the fjord to the inner part of the fjord. A chi-square test on the real recapture distribution compared with a random-walk distribution based on pooled release data, proved significant ($P<0.0001$), indicating that Greenland halibut do not migrate randomly in the fjord system, but tend to aggregate at specific localities at certain times of the year. Pooling the data by ice-cover period (1st and 2nd quarters) and open-water period (3rd and 4th quarters) and weighing the distribution within each quarter equally also resulted in significantly different distributions between the real data and the random-walk data. The real pooled data, shown by quarters (Fig. 4), demonstrated that Greenland halibut display a dispersed distribution during the ice-cover period (1st and 2nd quarters) but concentrate in the inner parts of the fjords during the open-water period (3rd and 4th quarters). The steep gradient from the 4th to the 1st quarter may be due to the fishing practices of the commercial fisheries, which are virtually dormant between November and February. Thus fish recaptured from the fishery for the two quarters mainly represent only the months of October and March, respectively .

Discussion

Sampling by hook-and-line gear does not reflect the true abundance of Greenland halibut in prespawning and spawning conditions. But, because the majority of the tagging took place outside the spawning period (winter and early spring), the sampling gear should not have biased any recovery patterns. Tagging in the southwest Greenland fjords took place in January, but the recovery pattern for those areas was confirmed by tagging data from other seasons of the year (Riget and Boje, 1989). Therefore, I assumed that any tagged specimens represent feeding fish, not spawning groups of the population.

Although Greenland halibut demonstrated long-distance displacements of about 2500 km in a two-year period, most recoveries indicated rather limited movement. The majority of tagged and recaptured Greenland halibut in this study support the current understanding of stock relationships among Greenland halibut populations (Bowering and Brodie, 1995; Boje et al., 1997; Vis et al., 1997). However, several cases of single recoveries suggest links between halibut populations not considered before. One fish recorded off Newfoundland had been released in Godthaab Fjord two years earlier, yet currently it is believed that Greenland halibut from Godthaab Fjord and other fjords of southwestern Greenland originate from the Icelandic spawning stock (Smidt, 1969; Riget et al., 1989; Boje, 1993). Released Greenland halibut from Baffin Bay yielded single recoveries in the northwestern Greenland fjord of Torsukkattak and in Denmark Strait. The latter is a migration distance of about 2500 km. Also, one Greenland halibut released in eastern Greenland at

[5] Simonsen, C. S., and J. Boje. 2000. An assessment of the Greenland halibut stock component in NAFO Division 1A inshore. NAFO (Northwest Atlantic Fisheries Organziaton) SCR Doc. 00/47, ser. N4278, 37 p. NAFO Secretariat, 2 Morris Drive, P. O. Box 638, P. O. Box 638, Dartmouth, Nova Scotia, Canada B2Y 3Y9.

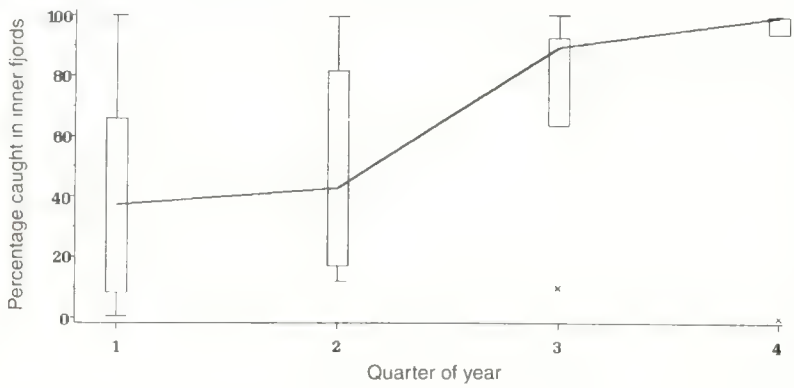

Figure 4

Box plot of proportion of Greenland halibut recaptured in the inner part of fjords in relation to those recaptured in the entire fjord system shown by season, according to pooled tagging-recapture data. Median values are joined by a solid line, boxes represent 25th and 5th percentiles, and horizontal "whiskers" represent 95% confidence limits. Outliers are indicated by crosses.

Ammassalik was recaptured north of the Faroe Islands four years after release, which indicates a link between the Greenland halibut populations in the Northwest Atlantic and those in the Northeast Atlantic and suggests some intermingling of halibut populations in the Atlantic Ocean. Studies on genetic differentiation have shown that Greenland halibut in the North Atlantic are genetically homogenous, indicating that populations do intermingle (Riget et al., 1992; Vis et al., 1997). Tagging experiments in Icelandic waters (Sigurdsson, 1981) included recoveries at long distances east of the release sites (Norway), even to the Barents Sea, also suggesting that there are interactions between the Northwest Atlantic and the Northeast Atlantic populations of Greenland halibut.

The 17 Greenland halibut recovered in Denmark Strait from tagging sites in West Greenland indicated a mix between West and East Greenland stocks, confirming previous work, especially tagging studies by Smidt (1969) and Boje[2] who documented recaptured Greenland halibut off western Iceland from releases in the Godthaab and Licthenau fjords of southern Greenland. Genetic studies and studies using parasites as natural tags (Riget et al., 1992; Boje et al., 1997) have shown that Greenland halibut in the fjords of southwestern Greenland differ considerably from offshore fish in Davis Strait. Riget and Boje (1988) hypothesized that young Greenland halibut in the southernmost coastal areas of western Greenland originate from different spawning grounds than those in the northern part of western Greenland. Larval distribution studies provide additional information on a link between the populations of southwestern Greenland and those of Denmark Strait. Magnusson's[6] data and more recently data on Icelandic 0-group Greenland halibut, 1970–97 (Hjörleifsson[7]) have provided evidence of larvae in a continuous belt from the Icelandic spawning grounds westward along the continental slope of eastern Greenland and southward to Cape Farewell. From pelagic Greenland halibut eggs and larvae in the western and southeastern Greenland areas, Smidt (1969) distinguished two groups of larvae with different growth patterns and hypothesized the intermingling of larvae from two different spawning areas, namely the spawning complex in Davis Strait and the stock west of Iceland (Denmark Strait). These authors have suggested that Greenland halibut eggs and larvae are transported by the East Greenland Current from Denmark Strait to the southernmost areas of western Greenland, a route shown earlier for cod (Tåning, 1937; Buch et al., 1994).

The behavior of Greenland halibut tagged in the fjords of northwestern Greenland is quite remarkable. The majority have remained within 50 km of release sites, even up to eight years after release and very few fish have undergone large-scale migrations of 100 to 500 km. Greenland halibut released from the fjords of northwestern Greenland have never been reported outside the fjord areas, but apparent residency may also be the result of almost no fishing activity in Baffin Bay (area adjacent to Uummannaq and Upernavik fjord). However, an assumed spawning migration to Davis Strait, is not plausible because a considerable fishery has developed in this area since the late 1980s (Anonymous, 1998). My data are consistent with the general assumption that Greenland halibut in the fjords of northwestern Greenland are recruited from the Davis Strait spawning stock (Smidt, 1969, 1998; Riget et al., 1989) and that adults thereafter remain resident in the fjords, i.e. do not undertake any significant spawning

[6] Magnusson, J. 1977. Notes on eggs and larvae of Greenland halibut at Iceland. ICES (International Council for the Exploration of the Sea) C.M. 1977/F:47, 6 p. ICES, Palægade 2-4, DK-1261 Copenhagen K, Denmark.

[7] Hjörleifsson, E. 1999. Personal commun. Marine Research Institute, P.O. Box 1390, Skúlagata 4, IS-121 Reykjavík, Iceland.

migrations. Some spawning and spent specimens have been observed in the fjords (Smidt, 1969; Riget et al., 1989; Nielsen and Boje[8]) and therefore spawning may occur in the fjords, at least sporadically. However, low bottom temperatures in the fjords probably inhibit the maturation process (Jensen, 1935; Templeman, 1973).

The seasonality apparent in local migrations for fish in the fjords of northwestern Greenland (Fig. 4) is presumed to correlate with feeding behavior. Allthough information is not available on the seasonality of prey organisms for Greenland halibut in the fjords, seasonal patterns for primary production are expected to affect other trophic levels in the food chain. Seasonality is reflected in the practices of the fishery; it tends to be concentrated in the inner part of the fjords during summer and more dispersed during winter near cities and human settlements (Simonsen and Boje[5]).

Davis Strait tagging data demonstrated that Greenland halibut within this area migrate widely and show no distinct patterns in orientation of movement. Such movements could be associated with spawning as suggested by Bowering (1984), i.e. a northward migration of Greenland halibut tagged in Newfoundland and Labrador to a proposed spawning area in Davis Strait. Jørgensen (1997) also found indications of movements during six years of a survey series, which he interpreted as seasonal movements between feeding areas and spawning grounds in the eastern part of Davis Strait. The wide migrations of offshore Greenland halibut as observed in the present study, i.e. within Davis Strait and from Davis Strait and Godthaab Fjord to Newfoundland, lend support to a proposed relationship between adult movements and spawning behavior.

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Abstract—Marine mammal diet is typically characterized by identifying fish otoliths and cephalopod beaks retrieved from stomachs and fecal material (scats). The use and applicability of these techniques has been the matter of some debate given inherent biases associated with the method. Recent attempts to identify prey using skeletal remains in addition to beaks and otoliths are an improvement; however, difficulties incorporating these data into quantitative analyses have limited results for descriptive analyses such as frequency of occurrence. We attempted to characterize harbor seal (*Phoca vitulina*) diet in an area where seals co-occur with several salmon species, some endangered and all managed by state or federal agencies, or both. Although diet was extremely variable within sampling date, season, year, and between years, the frequency and number of individual prey were at least two times greater for most taxa when prey structures in addition to otoliths were identified. Estimating prey mass in addition to frequency and number resulted in an extremely different relative importance of prey in harbor seal diet. These data analyses are a necessary step in generating estimates of the size, total number, and annual biomass of a prey species eaten by pinnipeds for inclusion in fisheries management plans.

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Improving pinniped diet analyses through identification of multiple skeletal structures in fecal samples

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Increases in marine mammal populations in Washington and Oregon have coincided with decreases in wild salmon populations in these and other western states. Recently, several salmon stocks in the western U.S. have been listed as threatened, endangered, or are under status review. These include coastal Oregon coho (*Onchorhyncus kisutch*), upper Columbia River steelhead (*O. mykiss*), and Snake River spring and fall chinook (*O. tshawytscha*), steelhead, and sockeye salmon (*O. nerka*; NMFS, 1997). Salmon often co-occur with marine mammals and predation may substantially reduce fish populations (Gearin et al., 1986). In these circumstances, an understanding of pinniped diet becomes necessary for the management of endangered fish populations. In 1994, the National Marine Mammal Laboratory began a project to quantify harbor seal (*Phoca vitulina*) predation on salmon in the lower Columbia River and to incorporate marine mammals in salmonid population models. Harbor seals are the most abundant pinniped in the lower river and annual maximum counts can exceed 2000 on the largest haul-out site, a tidal sandbar adjacent to Astoria, Oregon.

Pinniped prey are typically identified from fish sagittae (otoliths) recovered from fecal material (scat) and stomach contents (Brown, 1980; Harvey, 1989; Peirce and Boyle, 1991; Ochoa-Acuña and Francis, 1995; Beach et al.[1]). These methods yield biased results because of partial or complete digestion of otoliths and because of greater probabilities of recovering otoliths from larger individuals and species with robust otoliths and of identifying otoliths of species with distinctive morphological characteristics (Harvey, 1989; Gates and Cheal, 1992; Cottrell et al., 1996; Tollit et al., 1997; Bowen, 2000). Estimates of harbor seal predation on adult salmonids are particularly poor due to extremely low recovery (because the otoliths are small and fragile) and because harbor seals may not completely ingest large prey and thus otoliths may not be ingested (Pitcher, 1980; Harvey, 1989; Boyle et al., 1990; Harvey and Antonelis, 1994; Cottrell et al., 1996; Riemer and Brown, 1997).

We describe harbor seal diet on the lower Columbia River during spring, summer, and fall from 1) otoliths and 2) other skeletal elements (cranial bones, vertebrae, teeth, gill rakers, etc.) to examine potential differences in the diet characterized by the two methods. In previous studies, identification of all

[1] Beach, R. J., A. C. Geiger, S. J. Jefferies, S. D. Treacy, and B. L. Troutman. 1985. Marine mammals and their interactions with fisheries of the Columbia River and adjacent waters, 1980–1982. NWAFC (Northwest Alaska Fisheries Science Center) processed rep. 85-03, 316 p. NWAFC, National Marine Fisheries Service, Seattle, WA.

skeletal elements resulted in at least two times greater frequency of occurrence of some prey taxa than frequencies exclusively derived from otoliths (Riemer and Brown, 1997; Boyle et al., 1990; Cottrell et al., 1996). For major prey taxa, we estimated frequency of occurrence and minimum number of individuals from fish otoliths and other skeletal remains recovered from scats and average mass from otoliths.

Methods

During 1995, 1996, and 1997, scats were collected from Desdemona Sands (river km 26, 123°52′W,46°13′N), the largest harbor seal haul-out site in the lower Columbia River (Huber[2]). Scats were collected intermittently during 1995. From March through August 1996 and from March through October 1997, we attempted to collect 50 harbor seal scats every two weeks at extreme low tides. This sampling period coincided with Columbia River runs of spring, summer, and fall chinook salmon. Scats were collected from haul-outs, and upon arrival at the laboratory were rinsed in nested sieves (2-mm, 1-mm, and 0.5-mm mesh width). All skeletal elements were recovered, dried, and stored in vials. Cephalopod remains were stored in 70% isopropyl or ethyl alcohol. Other invertebrate remains were relatively rare (≤2% frequency of occurrence) and their contribution to the diet was disregarded because of difficulties enumerating individuals and determining primary from secondary (prey within large, ingested fishes) prey. Otoliths were identified to lowest possible taxon, their anatomical location recorded (left or right side), and enumerated (number for left side and number for right side). Lengths of intact left or right otoliths were measured parallel to the sulcus to the nearest 0.1 mm with an ocular micrometer. Micrometer measurements were verified with hand-held calipers. Other skeletal structures (such as teeth, vertebrae, and cranial bones) were identified to lowest possible taxon by comparing prey remains to reference samples (NMML[3]).

Scat collections were divided into three seasons: spring (samples collected prior to 15 May), summer (samples collected from 15 May to 15 July), and fall (samples collected after 15 July). These dates distinguish runs of spring, summer, and fall chinook salmon crossing the Bonneville Dam (river km 235), less two weeks estimated for travel from the lower Columbia River (Fryer, 1998). For each season, harbor seal diet was described by frequency of occurrence (FO), minimum number of individuals (MNI), and average prey mass estimated from otoliths of all major prey taxa. Frequency of occurrence (FO) of prey taxon j in season k was defined as

$$FO_{jk} = \frac{\sum_{i=1}^{s_k} O_{ijk}}{s_k},$$

where O_{ijk} = a binary variate indicating presence (1) or absence (0) of taxon j in sample i in season k; and

s_k = the total number of scats containing identifiable prey remains in season k.

Rare prey taxa were grouped with similar taxa for analyses. Unknown prey remains that were clearly distinct from known taxa were considered "unidentified taxa" in samples containing "identified" hard parts. Scats containing skeletal remains considered "unidentifiable," i.e. extremely eroded bone or fragmented material, were excluded from analyses. The minimum number of individuals (MNI) was estimated from the greatest number of left or right otoliths and unique or paired bone structures and expressed within each season as total MNI or average MNI per scat (total MNI/number of scats collected). Presence of non-unique fish remains (non-unique vertebrae, gillrakers, teeth) constituted a single individual. For example, if a scat sample contained five left otoliths, three right otoliths, and six atlas or axis vertebrae of a prey taxon, the MNI was six. FO and MNI were calculated from otoliths and again from all prey remains. Prey masses were estimated for the three seasons from allometric relationships between otoliths and body size (Harvey et al., 2000; Table 1). If relationships were unavailable for a species, regressions generated for a similar species were used. Otolith lengths were multiplied by a species-specific correction factor when available or an average correction factor to account for reduction in length due to digestion (Harvey, 1989). All intact left or right otoliths of a prey taxa were measured, and estimated masses were averaged for each season.

Suitable morphometric regressions were not available for several salmon species or did not include juvenile fish; therefore, we generated regressions including subadult age classes specifically for our study. In addition to published regressions, relationships between salmon otoliths and fish mass used in this study were calculated from National Marine Mammal Laboratory reference samples, the private collections of Walker[4] and NRC[5] (Table 1). Because of the large discrepancy in masses of adult and juvenile salmonids, otoliths were identified to species and classified as adult or juvenile according to species-specific lengths estimated from regression equations. "Adults" described all returning upriver migrants, including reproductively mature individuals and jacks. "Juveniles" were seaward migrants and may have included two-year-old fish of some species (Groot and Margolis, 1991). *Onchorhyncus*

[2] Huber, H. R. 1997. Unpubl. data. National Marine Mammal Laboratory, 7600 Sand Point Way NE, Seattle, WA 98115.

[3] NMML (National Marine Mammal Laboratory). 1997. Marine Mammal Prey Osteological Reference Collection. National Marine Mammal Laboratory, 7600 Sand Point Way NE, Seattle, WA 98115.

[4] Walker, W. 1998. Unpubl. data. National Marine Mammal Laboratory, 7600 Sand Point Way NE, Seattle, WA 98115.

[5] NRC (National Resources Consultants). 1998. Unpubl. data. Natural Resources Consultants, Inc., 4055 21st Ave. W, Suite 100, Seattle, WA 98119.

Table 1

Predicted standard length ($L=a+bx$; L=estimated standard length [cm], x=otolith length [mm]) and weight ($W=cL^d$; W=estimated weight [g], L=estimated standard length) of common harbor seal prey and sources of data. Calculations for groups of fish are based on species (in parentheses). Sockeye salmon calculations are based on regressions for silver salmon.

		Length		Weight		
Taxon	Species	a	b	c	d	Source
Ammodytidae	Pacific sand lance	0.727	0.137	0.0529	3.46	NMML[1]
Clupeidae	Pacific herring	−1.85	5.24	0.0044	3.398	Harvey et al., 2000.
	American shad	−11.08	11.46	0.0135	3.046	Harvey et al., 2000.
Cottidae	Pacific staghorn sculpin	−2.26	2.58	0.011	3.229	Harvey et al., 2000.
Embiotocidae	shiner surfperch	−0.52	1.74	0.01	3.515	Harvey et al., 2000.
Engraulidae	northern anchovy	0.85	2.28	0.0485	2.413	Harvey et al., 2000.
Gadidae	Pacific hake	0.96	2.04	0.0081	2.966	Harvey et al., 2000.
Gadidae	Pacific tomcod	−3.51	1.77	0.0064	3.191	Harvey et al., 2000.
Hexagrammidae	Hexagrammids (lingcod)	−6.03	8	0.0023	3.567	Harvey et al., 2000.
Osmeridae	whitebait smelt	3.02	2.11	0.0063	3.233	Harvey et al., 2000.
	eulachon	−2.7	4.71	0.0077	3.075	Harvey et al., 2000.
Pleuronectidae	Dover sole	12.23	2.75	0.0094	3.092	Harvey et al., 2000.
	English sole	−2.76	3.82	0.0163	2.939	Harvey et al., 2000.
	rex sole	−2.5	4.8	0.0238	2.692	Harvey et al., 2000.
	slender sole	1.08	3.37	0.0058	3.293	Harvey et al., 2000.
	starry flounder	0.23	3.35	0.0107	3.268	Harvey et al., 2000.
Salmonidae	chinook salmon	−10.4	6.73	0.0043	3.207	length: Walker[2]; weight: NRC[3]
	cutthroat trout	−91.2	89.3	0.0155	2.97	Walker[2]
	silver salmon	3.29	9.33	0.0103	3.092	length: NRC[3]; weight: Harvey et al., 2000.
	sockeye salmon (silver salmon)	3.29	9.33	0.0103	3.092	length: Walker[2]
	steelhead salmon	−32.43	14.77	0.0275	2.895	Harvey et al., 2000.
Scorpaenidae	rockfishes (black rockfish)	8.7	1.6	0.1225	2.499	Harvey et al., 2000.
Stichaeidae and Pholididae	gunnel and prickelback (wattled eelpout)	12.42	5.22	0.0007	3.483	Harvey et al., 2000.
	gunnel and prickelback (Pacific sand fish)	−4.57	6.06	0.0171	2.953	Harvey et al., 2000.

[1] NMML (National Marine Mammal Laboratory). 1997. Marine Mammal Prey Osteological Reference Collection. National Marine Mammal Laboratory, 7600 Sand Point Way NE, Seattle, WA. 98115.

[2] Walker, W. 1998. Unpubl. data. National Marine Mammal Laboratory, 7600 Sand Point Way NE, Seattle, WA 98115.

[3] NRC (National Resources Consultants, Inc.). 1998. Unpubl. data. National Resources Consultants, Inc. 4055 21st Ave. W, Suite 100, Seattle, WA, 98119.

clarki, O. kisutch, O. nerka, and *O. mykiss* less than 30 cm in length and *O. tshawytscha* less than 35 cm in length were considered seaward migrating juveniles (Groot and Margolis, 1991). All distinguishable salmon otoliths were identified to species and all identifications were verified by W. Walker.

Annual and seasonal variations in frequency of occurrence (FO) were examined with generalized linear models (Venables and Ripley, 1994). We limited our analyses to prey taxon with FO >5% during one or more seasons. Frequency of occurrence on each sampling date was modeled as a binomial random variable and for each prey taxon, we fitted five models: constant, season (S), year (Y), season+year ($S+Y$), and season+year with interactions ($S\times Y$). To account for overdispersion, we scaled Akaike's information criterion (AIC) using b=residual deviance/degrees of freedom from the $S\times Y$ model (Venables and Ripley, 1994). The model with the smallest scaled AIC was considered the best descriptor of seasonal and annual variation in FO.

Results

Over 1500 scats were collected from March 1995 through October 1997. Sample sizes varied among years and within season (Table 2). Frequency and number of indi-

Table 2

Sample collection dates, harbor seal scats with some identifiable prey remains, without any identifiable remains, and without remains for samples collected from Desdemona Sands 1995 through 1997. Spring (<15 May), summer (15 May to 15 July), and fall (>15 July) designate timing of chinook salmon runs on the Columbia River.

			Harbor seal scats		
Season	Collection date		With identifiable remains	Without identifiable remains	Without remains
Spring	5 Mar 1995		13	1	0
	5 Mar 1995		29	2	0
	14 Mar 1996		29	1	1
	21 Mar 1996		11	1	1
	10 Apr 1996		42	4	0
	2–8 May 1996		44	2	1
	11 Mar 1997		16	1	0
	26 Mar 1997		7	4	0
	10–11 Apr 1997		29	7	1
	15 Apr 1997		22	6	0
	28 Apr–1 May 1997		28	4	11
	9–10 May 1997		45	6	12
		Subtotal	315	39	27
Summer	18–19 May 1995		53	1	4
	14–16 Jun 1995		81	1	0
	28–29 Jun 1995		78	1	0
	14 Jul 1995		32	3	0
	30–31 May 1996		53	2	1
	18–19 Jun 1996		50	1	1
	2 Jul 1996		52	3	0
	27 May 1997		34	6	10
	6 Jun 1997		24	8	0
	23 Jun 1997		47	8	9
	8 Jul 1997		74	2	1
		Subtotal	578	36	26
Fall	15 Aug 1996		78	1	0
	29 Aug 1996		59	2	0
	22 Jul 1997		64	5	6
	4 Aug 1997		102	1	0
	19 Aug 1997		56	1	0
	3 Sep 1997		51	5	0
	16 Sep 1997		41	6	0
	16–17 Oct 1997		41	6	0
		Subtotal	492	27	6
	Total		1385	102	59

viduals consumed by harbor seals on the Columbia River were extremely variable, even among sample collections fewer than two weeks apart. Effort and sample sizes were unequal for season and years but we chose to include all data to better describe harbor seal diet. More than 45 prey taxa were described in 1385 samples with identifiable prey remains; however, most of the diet by number and frequency was composed of about 17 prey taxa (Table 3). Seasonal effects were important for 15 of 17 harbor seal prey with FO ≥5% (Table 3). Annual effects also were important for FO of lamprey (*Lampetra* spp.), Pacific hake (*Merluccius productus*), and northern anchovy (*Engraulis mordax*), and year-season interactions were included for three prey taxa (Table 3). All taxa had variances of FO greater than predicted by a binomial model (over-dispersion values, b>1; Table 3).

Table 3

Total minimum number of individuals (MNI), frequency of occurrence (FO), significant differences in frequency of occurrence of major prey taxa identified from all skeletal remains recovered from harbor seal scat (*S* indicates season, *Y* indicates year, *S*×*Y* indicates interaction, and N indicates no effects), and an estimate of over-dispersion of the binomial model (*b*). Only taxa with FO. >0.05 in at least one season were examined.

	MNI (all remains)			FO (all remains)				
Prey taxon	Spring	Summer	Fall	Spring	Summer	Fall	Effect	*b*
Pacific herring	168	511	141	0.36	0.57	0.22	*S*	8.4
Pacific staghorn sculpin	256	170	284	0.41	0.19	0.25	*S*×*Y*	2.4
Smelt species	133	204	625	0.28	0.18	0.35	*S*	6.2
Pacific tomcod	66	73	251	0.18	0.09	0.39	*S*	7.2
Lamprey species	109	204	41	0.26	0.25	0.06	*S*+*Y*	2.0
Starry flounder	136	105	160	0.30	0.14	0.12	*S*×*Y*	2.7
American shad	36	108	116	0.11	0.19	0.22	*N*	6.1
Other flatfish	102	129	132	0.20	0.12	0.18	*S*	2.2
Pacific hake	30	72	136	0.09	0.12	0.28	*S*+*Y*	4.0
Shiner surfperch	26	131	69	0.07	0.18	0.08	*S*	2.2
Gunnel and prickelback	47	55	30	0.15	0.08	0.06	*S*	3.0
Juvenile salmonids	92	71	30	0.19	0.05	0.05	*S*	3.2
Northern anchovy	3	63	290	0.01	0.06	0.19	*S*+*Y*	2.9
Adult salmonids	22	33	50	0.06	0.04	0.10	N	4.6
Peamouth chub	12	63	41	0.03	0.08	0.05	*S*×*Y*	2.4
Pacific sand lance	37	18	11	0.10	0.03	0.02	*S*	1.5
Rockfish species	23	14	18	0.07	0.02	0.03	*S*	1.5

The inclusion of all skeletal elements recovered from scat increased the MNI and FO of all harbor seal prey taxa (Table 4). The FO more than doubled for most taxa and usually was more affected by including all prey elements than was the average MNI (Table 4). We compared the MNI of several common harbor seal prey estimated from all structures to an estimate based on the number of recovered otoliths multiplied by a species-specific correction factor for recovery rate (accounting for complete digestion of the otolith; Harvey, 1989, Fig. 1). A value of 1.0 indicated that the same estimate was derived from both methods, whereas 0.5 indicated that the MNI estimated from all structures was twice the estimate from otoliths.

Seasonal variation was also apparent in estimated prey mass (Table 5). In some instances, estimates were based on very few otolith measurements, values were taken from the literature, or mass was averaged from other seasons when no intact otoliths were recovered (Table 5). Because some species were difficult to discern or regression relationships were unavailable, species were grouped by phylogeny or size similarities (Table 5). Smelts (Osmerids) were pooled by family and mass was estimated from whitebait smelt (*Allosmerus elongatus*), the most abundant species by distinguishable otoliths, and eulachon (*Thaleichthys pacificus*), although longfin smelt (*Spirinchus thaleichthys*) and surf smelt (*Hypomesus pretiosus*) were occasionally identified in harbor seal scats. Although smelt otoliths could be distinguished by species, smelt bone could not. Smelt mass estimates were based on eulachon (in their relative proportion) and whitebait smelt because although less common than the other three similar size species, eulachon were much larger. Masses of juvenile and adult salmonids were estimated separately for five species identified in harbor seal scat, with the exception of sockeye salmon, which was represented by one otolith from an adult fish. Mass for sockeye was based on regressions generated for silver salmon. Cutthroat (*Onchorhyncus clarki*) and steelhead salmon (*O. mykiss*) were not often distinguishable by otoliths, and mass estimates were based on steelhead because of their numerical dominance in the lower Columbia River. The sticheid-pholid group included fish from a variety of families: three spine stickleback (*Gasterosteus aculeatus*), snake prickleback (*Lumpenus sagitta*), high cockscomb (*Anoplarchus purpurescens*), wattled eelpout (*Lycodes palearis*), Pacific sandfish (*Trichodon trichodon*), and saddleback gunnel (*Pholis ornata*). Although not taxonomically related, these species were seldom represented by otoliths, individuals were very small, and with the exception of gunnels, were rare by number and frequency (Table 4). Little has been published about relationships between otolith length and fish length or fish length and mass for

Table 4

Average minimum number of individuals (MNI) per scat (total number of individuals identified in all scats collected in a season/ total number of scats collected in a season) and frequency of occurrence (FO) for all skeletal remains and for otoliths exclusively for major prey taxa of harbor seals in the Columbia River during spring, summer, and fall. All = all skeletal remains.

	Spring				Summer				Fall			
	Average MNI/scat		FO		Average MNI/scat		FO		Average MNI/scat		FO	
Prey taxa	All	Otoliths	All	Otoliths	All	Otoliths	All	Otoliths	All	Otoliths	All	Otoliths
American shad	0.11	0.01	0.11	0.01	0.19	0.01	0.19	0.01	0.24	0.03	0.22	0.02
Cephalopod	0.01		0.01		0.02		0.02		0		0	
Elasmobranch	0.08		0.07		0.01		0.01		0.01		0.01	
Gunnel and prickelback	0.15	0	0.15	0	0.10	0	0.08	0	0.06	0	0.06	
Hexagrammid	0.02	0	0.02	0	0.01	0	0.01	0	0.03	0	0.03	
Lamprey species	0.35		0.26		0.35		0.25		0.08		0.06	
Northern anchovy	0.01	0	0.01	0	0.11	0.06	0.06	0.02	0.59	0.52	0.19	0.10
Other flatfish	0.41	0.25	0.20	0.07	0.16	0.03	0.12	0.03	0.28	0.12	0.18	0.06
Pacific hake	0.10	0.02	0.09	0.01	0.12	0.01	0.12	0.01	0.28	0.02	0.28	0.02
Pacific herring	0.53	0.24	0.36	0.09	0.88	0.52	0.57	0.21	0.29	0.16	0.22	0.09
Pacific mackerel	0.02	0	0.02	0	0	0	0	0	0.01	0	0.01	0
Pacific sand lance	0.12	0.06	0.10	0.04	0.03	0.01	0.03	0.01	0.02	0.02	0.02	0.01
Pacific staghorn sculpin	0.81	0.62	0.41	0.20	0.29	0.17	0.19	0.08	0.58	0.42	0.25	0.11
Pacific tomcod	0.21	0.09	0.18	0.06	0.13	0.05	0.09	0.02	0.51	0.24	0.39	0.13
Peamouth	0.04	0.02	0.03	0.01	0.11	0.06	0.08	0.03	0.08	0.05	0.05	0.02
Rockfish species	0.07	0.02	0.07	0.02	0.02	0.01	0.02	0	0.04	0.01	0.03	0.01
Salmon species—adult	0.07	0.04	0.06	0.03	0.06	0.04	0.04	0.02	0.10	0.02	0.10	0.01
Salmon species—juvenile	0.29	0.16	0.19	0.06	0.12	0.10	0.05	0.02	0.06	0.02	0.05	0.01
Shiner surfperch	0.08	0.04	0.07	0.02	0.23	0.15	0.18	0.05	0.14	0.10	0.08	0.04
Smelt species	0.42	0.31	0.28	0.12	0.35	0.30	0.18	0.11	1.27	1.21	0.35	0.21
Starry flounder	0.43	0.24	0.30	0.11	0.18	0.09	0.14	0.05	0.33	0.28	0.12	0.06
Unidentified flatfish	0.04	0.02	0.03	0	0.02	0	0.02	0	0.02	0	0.02	0

these families; rather than ignore their occurrence, these species were pooled and mass estimates were based on measurements of wattled eelpout and sandfish otoliths (Table 5). The family Scorpaenidae was composed mostly of juvenile fish (*Sebastes* and *Sebastelobus* spp.) which can seldom be distinguished to species from bones and otoliths. Mass estimates were based on black rockfish (*Sebastes melanops*; Table 5). Morphometeric relationships for peamouth (*Mylocheilus caurinus*) were unavailable in the literature. Peamouth are small, slender members of the minnow family, less than 36 cm in length, with a shape similar to several other small harbor seal prey. Mass was assumed to be less than 100 g. Hexagrammids included lingcod (*Ophiodon elongatus*) and greenlings (*Hexagrammos* spp.) also were poorly represented by otoliths. Mass was estimated from lingcod otoliths (Table 5). Because bones and otoliths were often difficult to identify to species, flatfish other than starry flounder were pooled and mass was calculated from the average of estimated masses of identified otoliths (rex sole, *Glyptocephalus zachirus*; English sole, *Pleuronectes vetulus*; Dover sole, *Microstomus pacificus*; rock sole, *Pleuronectes bilineatus*; slender sole, *Eopsetta exilis*) for each season. In contrast, starry flounder remains were easily identified and much more abundant than any other flatfish species (Table 4).

Several taxa were not represented by otoliths because they were completely digested or because the species lacked otoliths. No intact Pacific mackerel (*Scomber japonicus*) otoliths were recovered from scat and their mass was assumed to be less than 700 g, the upper limit reported by Eschmeyer and Herald (1983). Lamprey species included river (*Lampetra ayresii*) and Pacific lamprey (*L. tridentata*). Mass was estimated from the upper limit of outgoing Pacific and river lamprey from Pacific Northwest river systems (Beamish, 1980). Little information was available for predicting the mass of elasmobranchs; however, all elasmobranchs (spiny dogfish, *Squalus acanthias;* and skates, Rajidae) consumed by harbor seals appeared to be juveniles. Elasmobranch mass was extrapolated from a regression of vertebral centrum width on mass from another skate species (Zeiner and Wolf, 1993), yielding an upper estimate of 490 g. We assumed the mass of skates and spiny dogfish consumed by harbor seals to be of a similar size, and all less than 500 g. Cephalopod (*Loligo*

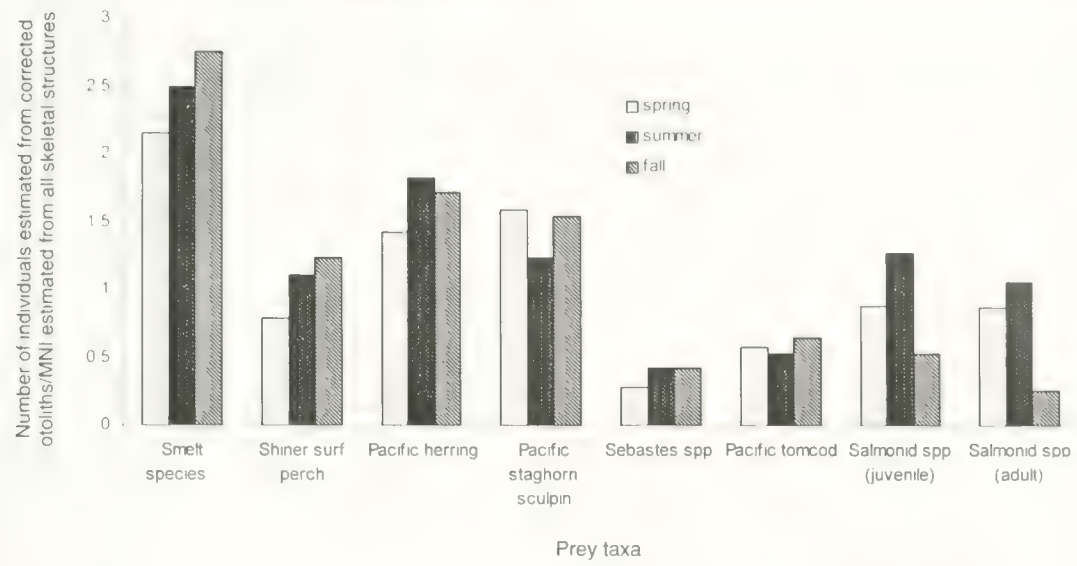

Figure 1

For eight prey taxa, ratio of estimated mean number of individuals estimated from the number of otoliths recovered from scat multiplied by a species-specific correction factor for recovery rate (Harvey, 1989) to MNI estimated from all structures recovered from harbor seal scats collected from Desdemona Sands during spring, summer, and fall 1995 through 1997. Values for smelt species are based on correction factors for eulachon. Values for salmonid species are based on correction factors for steelhead salmon.

opalescens and *Octopus* spp.) mass was estimated from regressions of beak measurements on mantle length and mass (Wolf, 1982).

Discussion

Diet of harbor seals in the Columbia River

Identification of prey remains indicated that the diet of harbor seals in the Columbia River was temporally variable and seals appeared to exploit prey when species were abundant. Many of the dominant prey by number and frequency were small fish such as herring, smelts, northern anchovy, juvenile flatfish, and sculpins (Tables 3 and 4). Pacific herring, Pacific staghorn sculpin (*Leptocottus armatus*), and smelts were three of the top six prey taxa by number and frequency for all three seasons (Table 4), although estimated masses varied greatly between season, indicating that seals preyed on different size classes (Table 5). Interestingly, scats without remains were most common during late spring and summer (Table 2). Olesiuk et al. (1990) reported similar results from British Columbia and suggested harbor seals were feeding on soft-bodied prey and roe. Occurrence of these scats in our study coincided with pupping on the lower Columbia River (Huber[6]), but an alternative explanation is that these may have been from nursing pups.

Most common harbor seal prey were variable by season or year (or both). Seasonal effects in the diet indicated periods when prey were reproducing, when young of the year were available, or perhaps an absence of highly abundant prey when seals relied more heavily on consistently available species. Annual differences in frequency of occurrence may have been largely the result of differences in sample timing or prey cohort strength (Moyle and Cech, 1982; Dark and Wilkins, 1994). Significant year and interactive effects between season and year probably reflected differences in prey year class (Table 3). For example, FO of anchovy (known to have high variability in recruitment) collected during fall of 1996 was 63%, whereas during fall of 1997 it was only 2%, although samples were collected on similar dates (Table 1). Harbor seals are generalist feeders and differences in frequency and number of prey probably reflect the temporal availability of prey rather than predator selection. This hypothesis is supported by AIC over-dispersion constants (b) greater than 1.0 for all prey taxa (Table 3). A binomial model assumes constant probabilities of a prey taxon occurring in scats collected on any sampling date within a season or year. Ephemerally abundant prey will have highly variable probabilities of occurrence in harbor seal scats collected in each season. It is likely that the overdispersion constant underestimates deviations for taxonomic groups, including more than one species such as salmonids and smelts, because temporal abundance of the different species in the group may be offset.

[6] Huber, H. R. 1997. Unpubl. data. National Marine Mammal Laboratory, 7600 Sand Point Way, NE, Bldg. 4, Seattle, WA 98115.

Table 5

Average mass (g) of harbor seal prey, standard deviation (SD), and number of otoliths measured (n) for spring, summer, and fall prey of harbor seals in the Columbia River. Boldface values are estimates calculated from other seasons (when no intact otoliths were recovered within a season) or from literature sources (when no structures were available for measurement).

		Spring			Summer			Fall		
Family	Prey taxa	Avg. mass	SD	n	Avg. mass	SD	n	Avg. mass	SD	n
Clupeidae	American shad	198	22	4	517	601	5	523	284	11
	Pacific herring	93	35	50	96	64	238	97	73	54
Engraulidae	Northern anchovy	9		1	12	2	30	14	5	192
Osmeridae	Smelt species	15	23	84	6	2	147	7	3	331
Gadidae	Pacific tomcod	128	115	24	180	106	25	228	132	107
	Pacific hake	67		1	421		1	446	292	2
Pleuronectidae	Starry flounder	70	117	64	114	243	52	89	168	101
	Other flatfish	181	100	35	181	111	42	225	82	35
Cottidae	Pacific staghorn sculpin	140	84	136	160	84	88	115	42	45
Salmonidae	Chinook juvenile	206	150	22	41	93	21			0
	Chinook adult	1385		1	8515	6854	2	6862	1757	4
	Cutthroat juvenile	225	56	7	255	66	6	315		1
	Cutthroat adult	509	51	7	426	52	2			0
	Silver juvenile	277		1			0	88	103	2
	Silver adult	1607	983	2	671	241	15	4317	3545	3
	Steelhead juvenile	488		1	283	81	2			0
	Steelhead adult	1637		1	897		1			0
	Sockeye adult	2832		1			0			0
Embiotocidae	Shiner surfperch	79	39	7	85	43	80	79	42	45
Stichaeidae and Pholididae	Gunnels and prickelbacks	**90**	**84**	0	97	38	3	84	127	3
Hexagrammidae	Hexagrammids	**2090**	**1727**	0	3410	1375	2	756	135	2
Scorpaenidae	Rockfish species	187	87	6	132	7	2	114		1
Ammodytidae	Pacific sand lance	72	63	3	62	58	8	151		1
Elasmobranchs	Elasmobranchs	**500**		0	**500**		0	**500**		0
Scombridae	Pacific mackerel	**700**		0	**700**		0	**700**		0
Petromyzontidae	Lamprey species	**50**		0	**50**		0	**50**		0
Ptychocheilus	Peamouth chub	**100**		0	**100**		0	**100**		0
Cephalopods	Cephalopods	**21**	**1**	0	**21**	**1**	0			0

Salmon in the harbor seal diet

Harbor seals consumed several species and sizes of salmon throughout our study, but frequency was greatest during spring. Size of otoliths recovered indicated that most of these fish were juvenile chinook and that adult salmon were consumed to a lesser extent, primarily during fall. Fryer (1998) reported no difference in mean fork lengths of adult spring–summer *O. tshawytscha* with scars from pinnipeds and those without scars at the Bonneville Dam and observed a greater percentage of fish with scars earlier in the year, although these findings do not necessarily contradict data from our study. Scarred fish represent failed predation and perhaps harbor seals attempted to capture fish beyond their ability when spring run-off results in greater water turbidity. In addition, part of the discrepancy may be due to the classification of "adult" salmon. For our purposes, we categorized all fish with estimated lengths greater than outgoing migrants (30 to 35 cm depending on the species) as "adults." The mean lengths of scarred spring-summer *O. tshawytscha* from 1994 to 1996 (75.9 to 79.3 cm standard length) were greater than the mean length of "adult" fish estimated from prey remains (73.4 cm mean standard length).

Riemer and Brown (1997) also examined all skeletal structures; however, their results summarized data for four years and 154 samples collected on eight dates. Riemer and Brown (1997) reported salmon FO as great as 39% for a single sampling date but found no salmonid remains in scats collected during February and March.

Table 6

Harbor seal prey taxa ranked by minimum number of individuals (MNI) estimated from all skeletal structures and otoliths, frequency of occurrence (FO) estimated from all skeletal structures and from otoliths, and average mass of prey estimated from allometric relationships between otoliths and fish size. Prey are ranked for all seasons; i.e. smelt are the most numerically abundant prey over spring, summer, and fall. Data (as opposed to ranks) are presented in Tables 4 and 5.

Prey taxa	MNI all	MNI otoliths	FO all	FO otoliths	Mass
Smelt species	1	1	3	1	21
Pacific staghorn sculpin	2	2	1	2	10
Pacific herring	3	4	1	3	15
Starry flounder	4	6	5	5	16
Other flatfish	5	7	8	7	7
Lamprey species	5		5		19
Pacific tomcod	7	7	5	6	8
American shad	8	15	4	14	4
Shiner surfperch	9	7	10	8	18
Pacific hake	10	14	9	14	
Salmon species—juvenile	11	10	12	10	6
Northern anchovy	12	3	15	4	20
Gunnel and prickelback	13		11		17
Cephalopod	14		13		13
Pacific mackerel	15		14		3
Salmon species—adult	16	12	15	12	1
Peamouth	16	11	17	11	12
Pacific sand lance	18	13	18	13	14
Rockfish species	19	16	19	8	10
Unidentified flatfish	20	4	20		
Elasmobranch	21		21		5
Hexagrammid	22		22		2

Monthly FOs were based on a single sampling collection. During our study, FO of juvenile salmon was 50% on a sampling date during March of 1997; however, no salmon remains were found in scats collected a week earlier during 1995. Additionally, we found salmonid remains in harbor seal scat during every month of our data collection and we found no significant differences in the seasonal occurrence of adult salmonids. This finding, however, may have been due to our grouping species.

Harbor seals eat Columbia River salmon; however, they feed mostly on juvenile fish during the spring, and otolith identifications have indicated that most of these are chinook salmon. Currently, salmonid bone cannot be identified to species; however, the National Marine Mammal Laboratory is investigating identification of salmonid species from skeletal remains by using genetic techniques.

Comparison of identification methods

Identifying and enumerating prey from all skeletal structures is more time consuming than relying exclusively on otoliths and the described diet may be substantially different. MNI and FO both increase when all structures are used, particularly for taxa such as Pacific tomcod (*Microgadus proximus*), Pacific hake, American shad (*Alosa sapidissima*), salmon spp., hexagrammids, elasmobranchs, and lampreys that are vastly underestimated from otoliths or are entirely lacking in otoliths (Table 4). Relative importance of prey in the diet also may be dramatically affected (Table 6). Prey of the greatest estimated masses are ranked among the least important prey by number and frequency with the use of all skeletal elements and these prey are often completely absent from the diet described from otoliths. If one were to rely solely on otolith identifications, these prey could be entirely overlooked. The extrapolation of estimated biomass of each prey taxa from average mass estimated by otolith length and MNI estimated from all skeletal remains has a variety of caveats—namely, the relative contribution of large, infrequent prey may be vastly underestimated by using otoliths.

Although the identification of all structures increases the magnitude of both MNI and FO, estimates of the number of individual prey are likely to be less accurate. A description of pinniped diet from all prey remains is subject to many of the same biases inherent in otolith identifications. Identification of all skeletal structures assumes an equal probabil-

ity of detecting all prey species and of recovering remains after consumption; these assumptions were violated to some extent in our study because, like otoliths, passage and identification of prey structures are taxon-specific (Harvey, 1989; Cottrell et al., 1996; Marcus et al., 1998). In captive experiments, herring (*Clupea pallasi*) were identified by 11 structures recovered in scats (other than otoliths), whereas smelt were represented only by vertebrae (Cottrell et al., 1996). Smelt vertebrae cannot be used to enumerate individuals, whereas several herring bones commonly recovered in scats are unique or are structures with definite sides (prootics, atlas and axis vertebrae), and even highly eroded herring bone retain characteristics identifiable to species. In contrast, bones of some taxa such as pleuronectids erode rapidly, losing species traits and are identified only to family. Given these factors, the identification of all skeletal structures represents the relative consumption of some prey more accurately than others. Further, MNI estimated from all skeletal structures is not corrected for complete digestion of structures useful for enumerating individuals. To date, there are no correction factors for complete digestion of bones and this lack, doubtlessly, is a source of substantial bias.

Behavior of both predator and prey also affects identification and enumeration of prey remains in scats. Small, schooling fish, such as smelts, are more likely to be consumed in greater numbers than larger, solitary fish such as hexagrammids. Smelts are most frequently identified from vertebrae; therefore MNI is more severely underestimated because more than one individual is likely to be consumed. Captive feeding studies also have indicated that the activity of the pinniped, its meal size, size of prey, and the physical structure of the prey bone all affect passage rate and the degree of erosion (Cottrell et al., 1996; Tollit et al., 1997; Marcus et al., 1998; Bowen, 2000).

The estimation of MNI from all prey structures recovered in scats presents a variety of complications; however, the alternative—using otolith correction factors—also has problems. Otolith correction factors based on recovery rates from feeding experiments are highly variable between repeated trials of the same individuals, different individuals, and different pinniped species (Harvey, 1989; Cottrell et al., 1996; Tollit et al., 1997; Bowen, 2000). Although his results were inconclusive, Bowen (2000) suggested that differences in activity levels may account for much of the variability in digestion (and correction factors). Activity levels among wild harbor seals are likely to be more variable than those between captive harbor seals with and without access to water, and thus otolith correction factors may yield erroneous estimates of individuals consumed by free-ranging predators. Limiting analyses of diet to qualitative measures such as FO will reduce the biases of including bone identification; however, the overall importance of frequent, small prey may be much less than indicated by their relative frequency.

Pinnipeds are considered generalist feeders and may feed on large numbers of abundant, frequently encountered prey; however, if mass is considered a measure of importance, they may be sustained by infrequent, large prey (Tables 4–6). A few prey species were both abundant and frequent (herring, smelts, sculpins, flatfish), yet their estimated masses were small. Large, infrequent species such as lingcod, hake, rockfish, and salmon may contribute more total mass to a hypothetical "meal." Unfortunately, these prey were also poorly represented by otoliths in our study and therefore our mass estimates may be inaccurate.

All methods of examining marine mammal diets, such as fecal analyses, stomach lavage, or stomach content analysis, are inherently biased to some degree. Biases of fecal analyses have been discussed at length in the literature; however, fecal analysis remains the least invasive and least expensive technique and allows for large sample sizes. Identification of all skeletal elements, rather than otoliths exclusively, is an improvement on other techniques. Although results are still subject to biases, prey taxa represented by hard parts in fecal material represent a minimum estimate of prey consumed. In addition, an examination of skeletal elements other than otoliths is mandatory for assessing the impact of harbor seals on certain prey species—protected salmon stocks, for example.

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Pinniped diet composition: a comparison of estimation models

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Abstract—Along the west coast of the United States, the potential impact of increasing pinniped populations on declining salmonid (*Oncorhynchus* spp.) stocks has become an issue of concern. Fisheries managers need species-specific estimates of consumption by pinnipeds to evaluate their impact on salmonid stocks. To estimate consumption, we developed a model that estimates diet composition by reconstructing prey biomass from fecal samples. We applied the model to data collected from harbor seals (*Phoca vitulina*) that are present year-round in the lower Columbia River where endangered stocks of salmonids pass as returning adults and as seaward-migrating smolts. Using the same data, we applied the split-sample frequency of occurrence model, which avoids reconstructing biomass by assuming that each fecal sample represents an equal volume of consumption and that within each sample each prey item represents an equal proportion of the volume. The two models for estimating diet composition yielded size-specific differences in consumption estimates that were as large as tenfold for the smallest and largest prey. Conclusions about the impact of harbor seal predation on adult salmonids, some of their largest prey species, remain uncertain without some appropriate rationale or further information (e.g. empirical captive studies) to discriminate between these models.

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During the last three decades, harbor seal (*Phoca vitulina*) and California sea lion (*Zalophus californianus*) populations along the west coast of the United States have increased dramatically (Forney et al., 2000). During the same period, numerous salmonid (*Oncorhynchus* spp.) stocks that are consumed by these pinnipeds have declined and some of these stocks have been classified as threatened or endangered (NMFS, 1997). To evaluate the impact of pinnipeds, fisheries managers need species-specific estimates of salmonid consumption by pinnipeds.

In some limited situations, pinniped prey consumption can be determined from direct observation if the pinniped brings the prey to the surface and feeding occurs in a few predictable areas (Bigg et al., 1990). However, in most situations, consumption estimates have relied on a less direct approach that uses estimates of pinniped energetic requirements, prey energy density, and pinniped diet composition (Olesiuk, 1993; Hammill et al., 1997; Stenson et al., 1997; Nilssen et al., 2000). In their simplest form, these models express biomass consumption of prey species i as $B_i = \xi\pi_i/\varepsilon_i$, where ξ is the total energy requirement of the pinnipeds, π_i is the proportion of the energy in the diet derived from species i, and ε_i is the energy density (kcal/g) of species i. The total energy requirement of a population depends on the size of the population and requirements of each seal, which vary by sex, age, and status (i.e. whether it is molting, pregnant, lactating). If prey energy density is constant or an average energy density is used, biomass consumption can be expressed as $B_i = \xi\pi_i$, where ξ is the total biomass requirement and π_i is the proportion of the biomass derived from species i. Valid estimates of pinniped energetic requirements and prey energy density are important, as well as accurate estimates of pinniped diet composition.

Diet composition can be determined from skeletal remains in scat (feces) and from stomach and intestinal contents, or stomach lavage. Each of these methods has some inherent bias (Bigg and Perez, 1985; Pierce et al., 1991). Examination of prey remains in scat is noninvasive and allows for the largest sample size. There are, however, numerous well-recognized problems in describing marine mammal diet from scats (Jobling, 1987; Harvey, 1989; Harvey and Antonelis, 1994; Tollit et al., 1997b; Marcus et al., 1998). In particular, nonrandom passage of hard parts, primarily otoliths, biases estimates of diet composition; however, the bias can be reduced by inclusion of all hard parts (e.g. bones) (Browne et al., 2002).

In 1994, we began an investigation of harbor seal consumption of salmonids in the lower Columbia River. Initial attempts to survey the lower 110 km stretch of the river to estimate adult salmonid consumption by direct observation proved infeasible. The only remaining noninvasive alternative was to develop a consumption estimate

based on analysis of scat collections. During 1995–97, harbor seal scats were collected at the Desdemona Sands haulout from 1 March to 15 October. By combining diet composition obtained from scat analysis and contemporaneous surveys of seal abundance, we estimated the average consumption of salmonids and other prey in the Columbia River by harbor seals during spring, summer, and fall of 1995–97.

In our study, we focussed on the method of estimating diet composition from a sample of scats. We describe an estimator for diet composition based on reconstruction of the prey biomass represented in the scat and show how it is related to an alternative estimator described by Olesiuk (1993). Using the data collected on harbor seals in the Columbia River, we demonstrate the sensitivity of the consumption estimates to the method for estimating diet composition.

Materials and methods

Diet composition models

If we could randomly select a sample of n prey items consumed by pinnipeds, a ratio estimator (Cochran, 1977) would be appropriate to estimate the proportion of biomass (π_i) represented by the i^{th} prey species from ω possible prey species:

$$\hat{\pi}_i = \frac{b_i}{\sum_{i=1}^{\omega} b_i} = \frac{n_i \overline{w}_i}{\sum_{i=1}^{\omega} n_i \overline{w}_i}, \quad (1)$$

where b_i = the total biomass of the n_i prey items that are species i;
$\overline{w}_i = b_i / n_i$ = the average mass for species i; and
$n = \sum_{i=1}^{\omega} n_i$.

Prey hard-parts in a scat represent a filtered selection of the prey species that were consumed by a single animal over some unknown and variable amount of time. Captive feeding studies have shown that a scat does not represent a single meal or even a single fixed period of feeding time (Harvey, 1989). Moreover, pinnipeds are unlikely to consume the same amount of prey in each meal or in a specified amount of time. Therefore, the biomass represented by the prey remains in a scat is unlikely to be constant because consumption varies. From a collection of s scats in which each scat represents a variable amount of biomass that is proportional to consumption, the ratio estimator (Eq. 1) is also appropriate, where b_i is the total biomass of species i from the s scats. We will refer to (Eq. 1) as biomass reconstruction (BR), which is equivalent to the estimator used by Harvey (1988) and Hammond and Rothery (1996).

Alternatively, one could argue that the biomass reconstructed from prey remains in a scat may vary for numerous reasons other than consumption. Variation in scat volume and production and the resulting amount of hard parts may be affected by factors that influence digestion and deposition (e.g. seal activity level). Also, it may not always be possible to collect an entire scat or even reasonably define a scat as a discrete entity. Thus, even though consumption by seals varies to some degree, the biomass reconstructed from a scat may vary much more than the variation in consumption. Thus, one could argue that each scat should be treated as a "representative" variable-size sample of a nearly constant amount of biomass consumed during some feeding interval. With that conceptual sampling model, the most appropriate estimator would be a simple average of the proportions in each scat:

$$\hat{\pi}_i = \frac{\sum_{k=1}^{s} \hat{\pi}_{ik}}{s} = \frac{\sum_{k=1}^{s} \left(\frac{b_{ik}}{\sum_{i=1}^{\omega} b_{ik}} \right)}{s} = \frac{\sum_{k=1}^{s} \left(\frac{n_{ik}\overline{w}_{ik}}{\sum_{i=1}^{\omega} n_{ik}\overline{w}_{ik}} \right)}{s} \quad (2)$$

where b_{ik} = the biomass of species i;
n_{ik} = the number of species i consumed; and
$\overline{w}_{ik}$ = the average mass of species i in the k^{th} scat.

Equation 2 is similar to the estimator of Olesiuk (1993), which he called split-sample frequency of occurrence (SSFO):

$$\hat{\pi}_i = \frac{\sum_{k=1}^{s} \left(\frac{I_{ik}}{\sum_{i=1}^{\omega} I_{ik}} \right)}{s}, \quad (3)$$

where I_{ik} = an indicator variable which equals 1 if one (or more) prey items of species i is in scat k, and 0 otherwise.

Equation 2 is equivalent to 3 when you make Olesiuk's (1993) assumption that an equal amount of biomass of each species in the scat was consumed. SSFO requires only a determination of the presence or absence of the prey in a scat, and thus, it is much easier to implement than either Equations 1 or 2, which require an enumeration of the individual prey in each scat and their mass.

Enumeration of prey in a scat sample is straightforward with unique structures such as otoliths. However, by using nonunique hard parts (e.g. gillrakers, vertebrae) to reduce selection bias resulting from unequal digestibility of otoliths, problems are introduced with enumeration. When prey are exclusively represented in scat by nonunique structures, it may be possible only to determine that a single individual was consumed or at best a minimum number can be constructed by enumerating nonunique structures and dividing by the average number of structures per fish (e.g. count of vertebrae divided by average number of vertebrae per fish). By including nonunique structures, enumeration of prey is replaced with an estimate of the

minimum number of prey ($\hat{n}_i$) consumed. For some hard parts, it may not be possible to identify the species, but the hard part can be classified to a group of species, such as family. In these cases, the species can be grouped into a single unit for estimation (e.g. all hexagrammids) or the unidentified prey can be partitioned to species based on the sample of species-specific hard parts. For example, most salmonid bones are currently indistinguishable to species; therefore salmonids in scats represented by bones (u) can be apportioned into species from proportions (γ_i) observed from otoliths (o_i). If we denote Ψ to be the set of all identified salmonids represented by otoliths, the number of salmonid prey in species i can be estimated as

$$\hat{n}_i = o_i + u\hat{\gamma}_i \quad \text{for } i \in \Psi. \tag{4}$$

where

$$\hat{\gamma}_i = \frac{o_i}{\sum_{i \in \Psi} o_i} \quad \text{for } i \in \Psi. \tag{5}$$

Prey mass can be determined from morphometric relationships between hard part dimensions (e.g. typically otolith length) and mass. Adjustments should be made to account for partial digestion of the hard part. From regressions between otolith length (corrected for degradation) and fish length and between fish length and mass, an estimate of the average mass of prey represented in scat can be constructed (Harvey et al., 2000; Browne et al., 2002). In some scats, a prey species may be represented only by hard parts (e.g. gillrakers) that do not have a quantifiable relationship to mass. We have to assume that the prey with unknown mass are represented by the average mass determined from the measurable hard parts (e.g. unbroken otoliths) of that species.

Thus, the biomass cannot strictly be measured but must be estimated by using estimated average mass ($\overline{w}_i$) and estimated number of individual prey ($\hat{n}_i$):

$$\hat{b}_i = \hat{n}_i \frac{\sum_{j=1}^{o_i^*} \hat{w}_{ij}}{o_i^*} = \hat{n}_i \overline{w}_i, \tag{6}$$

where o_i^* = the number of hard parts (typically unbroken otoliths); and
$\hat{w}_{ij}$ = the estimated mass derived from the regressions relating otolith length to fish mass.

To estimate number of prey consumed (P_i) rather than biomass, estimated biomass is divided by average mass:

$$\hat{P}_i = \frac{\hat{B}_i}{\overline{w}_i} = \xi \frac{\hat{\pi}_i}{\overline{w}_i} = \xi \hat{\rho}_i, \tag{7}$$

where $\hat{\rho}_i = \frac{\hat{n}_i}{\sum_{i=1}^{o} \hat{b}_i}$ = the number of prey species i consumed per unit of biomass consumed.

Pinniped diet can be quite variable in response to prey availability (Pierce et al., 1991; Tollit et al., 1997a; Browne et al., 2002; Beach et al.[1]; Brown et al.[2]). Because scat collected at a single date may reflect what was locally available at that time, collecting scats at different times throughout a season or year will provide a better representation of diet. From scats collected across several occasions, what is the best way to estimate average diet composition? If the amount of scat collected and resulting reconstructed biomass for an occasion is proportional to the amount of prey consumed, the data should be pooled for a single ratio estimate. However, in many cases the amount of scat collected will reflect a multitude of factors, such as tide height, storms, human disturbance, and the length of time that the seals were at the haulout prior to collection. Also, in many circumstances a fixed number of scats are collected rather than some fixed proportion of the scats available at the haulout. Therefore, we suggest that an average of the proportions (ratios) is appropriate. If there are T occasions, the average proportion is

$$\hat{\pi}_i = \frac{\sum_{t=1}^{T} \hat{\pi}_{it}}{T}. \tag{8}$$

Often there are seasonal shifts in diet resulting from prey availability (Olesiuk et al., 1990; Tollit and Thompson, 1996; Browne et al., 2002). In such cases, the analysis should be stratified by season. If data are collected over several years, again a simple average of the seasonal proportions is appropriate. In the appendix, we provide variance estimators for diet composition and consumption estimates for data collected over several years stratified by season.

Data collection and analysis

For the data used in this paper, Browne et al. (2002) have described the scat collection and analytical methods and have provided descriptions of the food habits from these data. As in Browne et al. (2002), we stratified our data collection and analysis into three seasons, spring (1 March–14 May), summer (15 May–15 July) and fall (16 July–15 October), based on the timing of chinook salmon runs at the Bonneville Dam, offset by two weeks to account for the travel of salmonids from the lower Columbia River to the Dam (at river km 235). We describe here additional meth-

[1] Beach, R. J., A. C. Geiger, S. J. Jefferies, S. D. Treacy, and B. L. Troutman. 1985. Marine mammals and their interactions with fisheries of the Columbia River and adjacent waters, 1980–1982. NWAFC Processed Rep. 85-03, 316 p. Northwest and Alaska Fisheries Sci. Cent., Nat. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE, Seattle, WA 98115.

[2] Brown, R. F., S. D. Riemer, and S. J. Jeffries. 1995. Food of pinnipeds collected during the Columbia River Area Commercial Salmon Gillnet Observation Program, 1991–1994. Wildlife Diversity Program Tech. Rep. 95-6-01, 16 p. Oregon Department of Fish and Wildlife, 2501 SW 1st Ave., PO Box 59, Portland, OR 92707.

ods for development of estimates of prey consumption by harbor seals.

Prey remains were usually identified to species, but in some cases could only be identified to genus, family, or larger taxon (e.g. flatfish). Our primary interest was salmonid consumption; therefore, where possible, we also classified salmonids as juvenile or adult. For non-salmonids, we were less interested in species-specific estimates of consumption; therefore we did not always identify nonotolith remains to species when identification was either time-consuming or uncertain. For example, we divided flatfish into starry flounder (*Platichthys stellatus*) and "other flatfish" because starry flounder were easily identified, but the remaining flatfish species were not easily distinguishable. In some cases, prey remains could be identified to species, but they occurred infrequently; therefore we grouped them by family (e.g. Hexagrammidae) or groups of families (e.g. Stichaeidae and Pholididae). We have used the term "prey group" to generically refer to our classification of prey remains into family (or more general taxon), species, or species and size.

Both species and size of salmonids could be determined from unbroken otoliths. For most salmonids, even broken otoliths were classified as adult or juvenile because of a very apparent discontinuity in otolith size between adults and juveniles. However, for coho salmon (*O. kisutch*) and cutthroat trout (*O. clarkii*), the size difference between juveniles and adults was less obvious; therefore we did not classify broken otoliths. We partitioned coho salmon and cutthroat trout broken otoliths into adults and juveniles according to the observed seasonal proportion of unbroken otoliths for each species. Salmonids represented exclusively by bone were not separated by species or size, but were apportioned according to seasonal average proportions measured from otoliths.

The lengths of all unbroken otoliths were measured to compute an average mass for most prey. We corrected the measured length for an average amount of degradation (Browne et al., 2002). For Pacific mackerel (*Scomber japonicus*), elasmobranchs (sharks and skates), lamprey (*Petromyzontid* spp.) and peamouth chub (*Mylocheilus caurinus*), size relationships were not available; therefore literature values of average mass were used (Browne et al., 2002). For many species, there were very few measurable otoliths for an individual collection date; therefore an average weight was computed across all collection dates within that particular season and applied to each collection date during that season. If there were 10 or fewer hard parts measured in each season, we used the average and variance of the predicted weights from the data pooled over the three seasons (i.e. we assumed no seasonal differences).

The amount of prey biomass (ξ) required to sustain the harbor seals in the Columbia River during a season is a function of seal abundance (N), the age and sex proportions (θ_a) and the sex- and age-specific daily biomass requirements of the seals (C_a), and the length of the season (D):

$$\xi = N \sum_a \theta_a C_a D. \tag{9}$$

We confined our analysis to nonpup (>6 months) seals because weaned pups comprise a small proportion of the seals in the Columbia River and they primarily consume soft-bodied prey or crustaceans (Pitcher, 1980; Riemer and Brown[3]) which could not be incorporated into our estimates of diet composition. The average number of seals was determined from aerial surveys that were flown over seal haulout sites. Pups and nonpups were counted from photographic slides or they were counted during flights over small haulout sites. Aerial surveys were flown on 10 occasions between March and July 1995, on 16 occasions between March and June 1996, and on 25 occasions between March and September 1997. In 1997, radio-tags and visual markers were attached to 26 seals (8 adult males, 10 adult females, and 8 subadults) to estimate the average proportion of nonpup seals that were hauled out during the surveys (f) with the techniques described by Huber et al. (2001). The correction factor was used for all of the counts to construct average seasonal abundance estimates. Abundance of nonpup seals in each season was estimated by

$$\hat{N}_j = \frac{\bar{c}_j}{f}, \tag{10}$$

where $\bar{c}_j$ = the average count of nonpup seals hauled out during season j.

Age (other than unmolted pups) and sex of seals cannot be determined from aerial surveys; therefore, estimating the sex and age structure would require capturing seals at different times throughout the year. Instead, we relied on a predicted sex and age structure based on life-history table data (Bigg, 1969; Pitcher and Calkins[4]), but rescaled the proportions to the nonpup portion of the population. We used the following sex and age structure for nonpup seals (θ_a): a=1, 23% subadult (1–4 yr); a=2, 35% adult males (>4 yr); a=3, 42% adult females (>4 yr). We assumed the following biomass requirements for the three groups: C_1= 1.89 kg/d , C_2= 2.37 kg/d, and C_3= 2.63 kg/d. We derived these values by averaging the age-specific daily biomass requirements given by Olesiuk (1993). We did not include any variability in our estimates of biomass requirements, nor did we include any uncertainty in the estimates of the population structure (θ_a). Therefore, variability in ξ only included variation in the population estimate.

[3] Riemer, S. D., and R. F. Brown. 1997. Prey of pinnipeds at selected sites in Oregon identified by scat (fecal) analysis, 1983–1996. Wildlife Diversity Program Tech. Rept. 97-6-02. 34 p. Oregon Department of Fish and Wildlife, 2501 SW 1st. Ave., PO Box 59, Portland, OR 92707.

[4] Pitcher, K. W., and D. G. Calkins. 1979. Biology of the harbor seal, *Phoca vitulina richardsi*, on Tugidak Island, Gulf of Alaska. Final Rep. to OCSEAP (Outer Continental Shelf Environmental Assessemnt Program), Dept. Interior, Bur. Land Manage., 72 p.

Table 1

Apportionment of unidentified salmonid remains based on proportions of identified salmonid remains as species i in season j (γ_{ij}).

		Proportions (γ_{ij})			Apportioned unidentified ($\gamma_{ij}u_j$)		
Species	Age class	Spring	Summer	Fall	Spring	Summer	Fall
Chinook	Adult	0.038	0.083	0.462	2.3	2.3	30.9
	Juvenile	0.538	0.389	0.077	31.8	10.9	5.2
Coho	Adult	0.051	0.292	0.231	3.0	8.2	15.5
	Juvenile	0.026	0.000	0.154	1.5	0.0	10.3
Cutthroat	Adult	0.144	0.049	0.000	8.5	1.4	0.0
	Juvenile	0.144	0.146	0.077	8.5	4.1	5.2
Sockeye	Adult	0.019	0.000	0.000	1.1	0.0	0.0
Steelhead	Adult	0.019	0.014	0.000	1.1	0.4	0.0
	Juvenile	0.019	0.028	0.000	1.1	0.8	0.0
Total (u_j)					59	28	67

Table 2

Average and coefficient of variation (in parentheses) of the count ($\bar{c}_j$) of hauled-out nonpup seals, estimated abundance (N_j) and prey biomass requirements (ξ_j) for each season.

Season	Avg. count	Abundance	Required biomass (t)
Spring (1 Mar–14 May)	1012 (0.11)	1659 (0.12)	296.34 (0.12)
Summer (15 May–15 July)	823 (0.07)	1349 (0.10)	193.65 (0.10)
Fall (16 July–15 Oct)	598 (0.15)	980 (0.16)	214.21 (0.16)

Results

Scats were collected on 31 occasions during March–October 1995–97 providing 1385 scats with identifiable prey remains (Browne et al., 2002). All seasons were sampled in each year except for the fall of 1995. Remains were identified from 5832 different prey which were assigned to ω=28 prey groups. We excluded the very minor unidentified component. Salmonids of unknown species and size represented by bone (154) were partitioned based on the observed seasonal proportions (Eqs. 4 and 5, Table 1).

During 16 of the flights in 1997, the proportion of the 26 radio-tagged seals hauled out was measured to construct a single average correction factor ($1/f$) of 1.64 (percent coefficient of variation (CV)=6.7%) to estimate seasonal abundance from the haulout counts (Table 2). Using the assumed age and sex structure and biomass requirements, we estimated that the seals in the Columbia River would consume 704 metric tons (t) of biomass during the 7.5 month period (Table 2).

From the 1385 scats, we reconstructed 1.15 t of biomass which was only 0.16% of the required biomass consumption. Because the number of scats and seals varied between seasons, the percentages varied from 0.077% in spring, 0.173% in summer, and 0.272% in fall. Using BR, we constructed diet composition estimates (Fig. 1) and seasonal consumption estimates (Fig. 2). Many of the estimates of salmonid consumption had exceedingly poor precision with the coefficient of variation exceeding 0.5 (Table 3). Using adult chinook salmon (*O. tshawytscha*) as an example, an examination of the variance components demonstrated that estimation of biomass (Table 4) was the predominant source of variance. Variance associated with biomass estimation includes variation in predicted weights and estimation of number of prey ($\hat{n}_i$) for salmonids. The latter accounted for one- to two-thirds of the total variance for salmonids depending on the species and size group. The use of genetics to obtain species identification of the unknown salmonids identified by bone would substantially improve the precision for salmonids.

Using BR to estimate diet composition, adult chinook salmon was the only salmonid that was consistently in the five most important prey items for each season based on percent of biomass (Fig. 1). Their importance was derived from their average mass which was the largest of all the prey. Adult chinook salmon and the other salmonids appeared much less important if the ranking was based on the number consumed (Fig. 2). Smaller prey items such as herring (*Clupeid spp.*), sculpin (*Leptocottus armatus*), lamprey (*Petromyzontid spp.*), smelt (*Osmeridae*) and

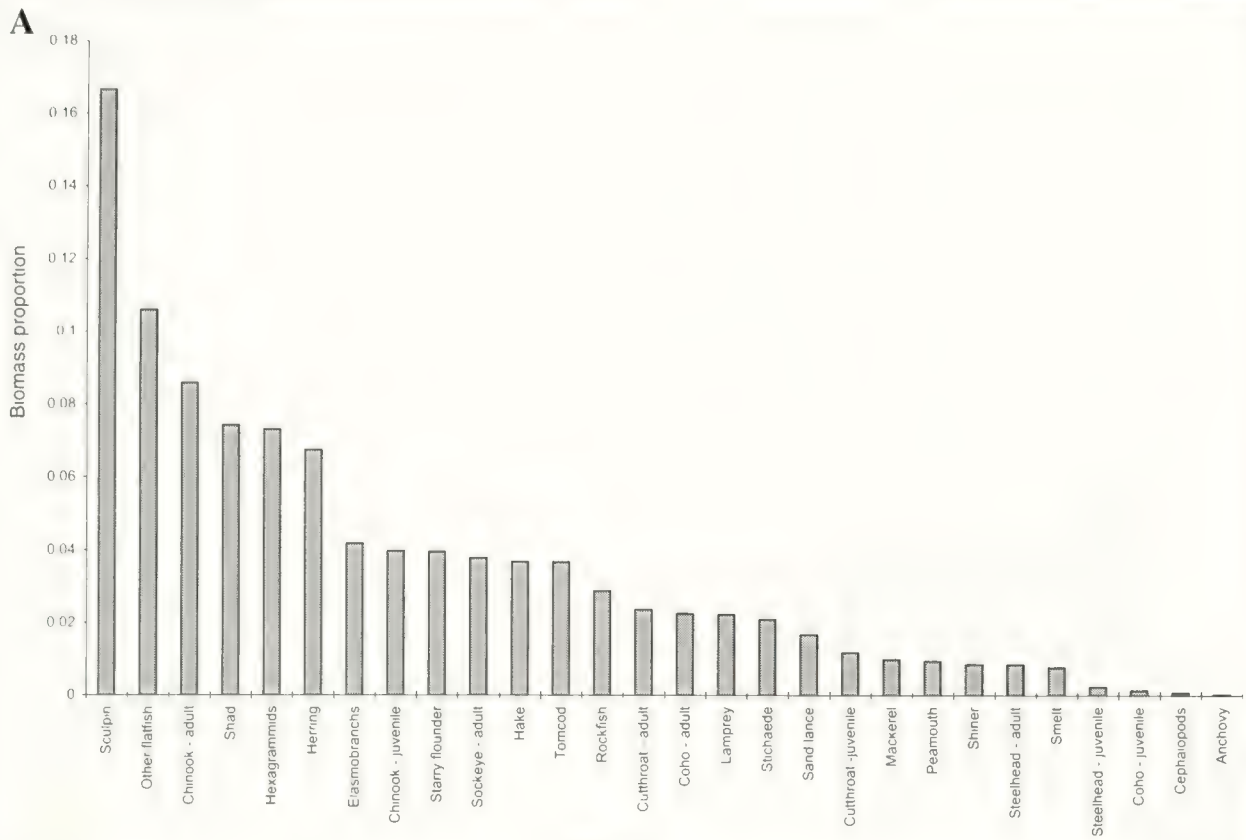


Figure 1

Average biomass proportion (π_i) of each prey group in the diet of harbor seals on the Columbia River between 1995 and 1997 for spring (**A**), summer (**B**), and fall (**C**).

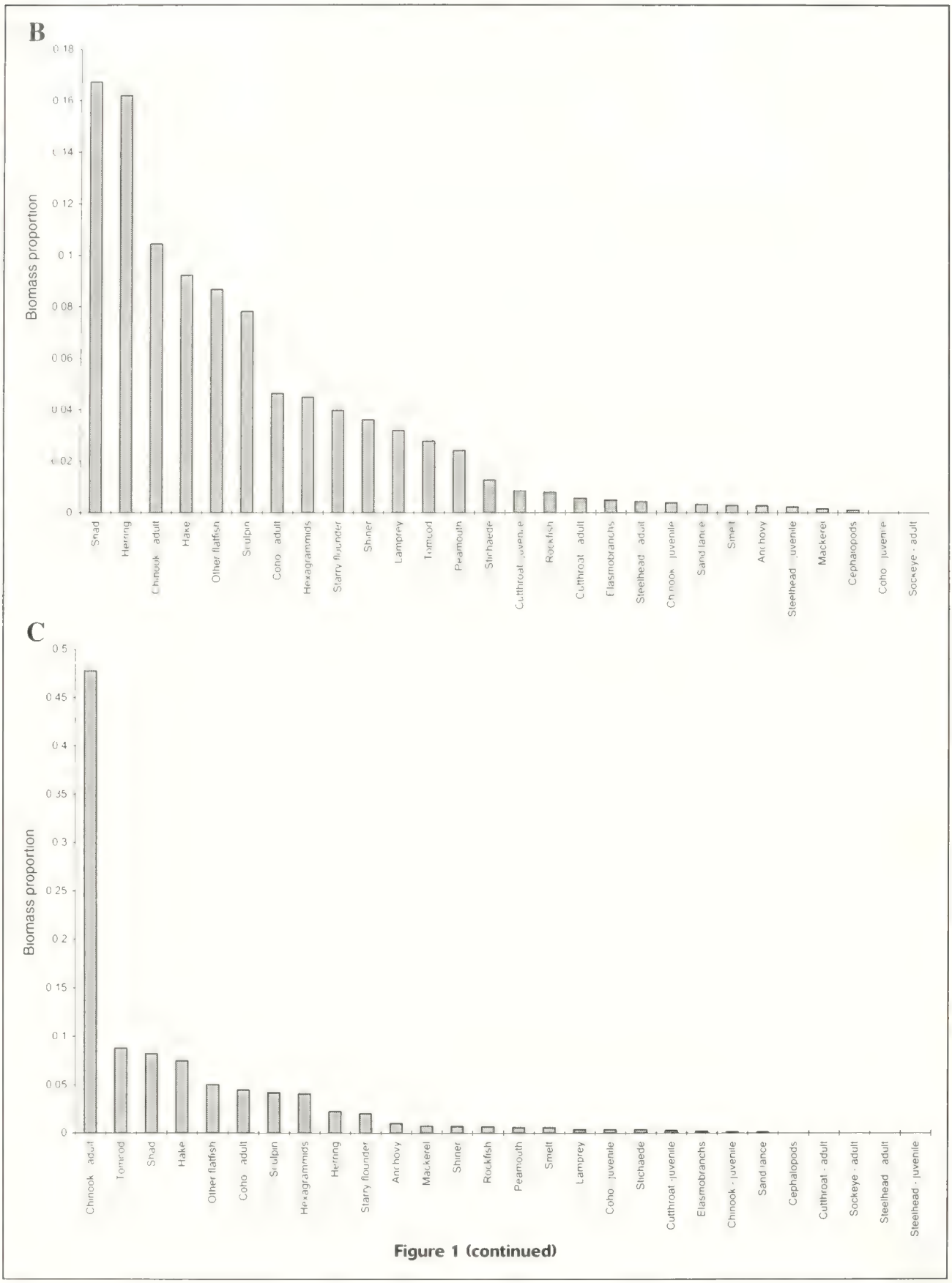
Table 3

Average seasonal estimates of the number of salmonids consumed by harbor seals during 1995–97 (P_i) (in 1000s) and its coefficient of variation (CV) based on the biomass reconstruction (BR) method for diet composition.

		Spring		Summer		Fall	
Species	Size	P_i	CV	P_i	CV	P_i	CV
Chinook (*O. tshawytscha*)	Adult	3.9	0.65	3.1	0.44	15.6	0.30
	Juvenile	57.1	0.39	18.0	0.32	2.4	1.11
Coho (*O. kisutch*)	Adult	5.1	0.73	13.3	0.32	7.3	0.65
	Juvenile	2.8	0.85	0.0	0.00	4.9	0.76
Cutthroat (*O. clarkii*)	Adult	14.2	0.40	2.2	0.42	0.0	0.00
	Juvenile	14.2	0.40	6.6	0.38	2.3	1.08
Sockeye (*O. nerka*)	Adult	4.4	0.45	0.0	0.00	0.0	0.00
Steelhead (*O. mykiss*)	Adult	2.0	0.99	0.6	0.64	0.0	0.00
	Juvenile	2.0	1.00	1.3	0.57	0.0	0.00

anchovy (*Engraulis mordax*) were consumed in greater quantity but they were not always a large proportion of the reconstructed biomass.

Using split-sample frequency of occurrence (SSFO) to estimate diet composition, the results were dramatically different for larger and smaller prey items (Fig. 3). For



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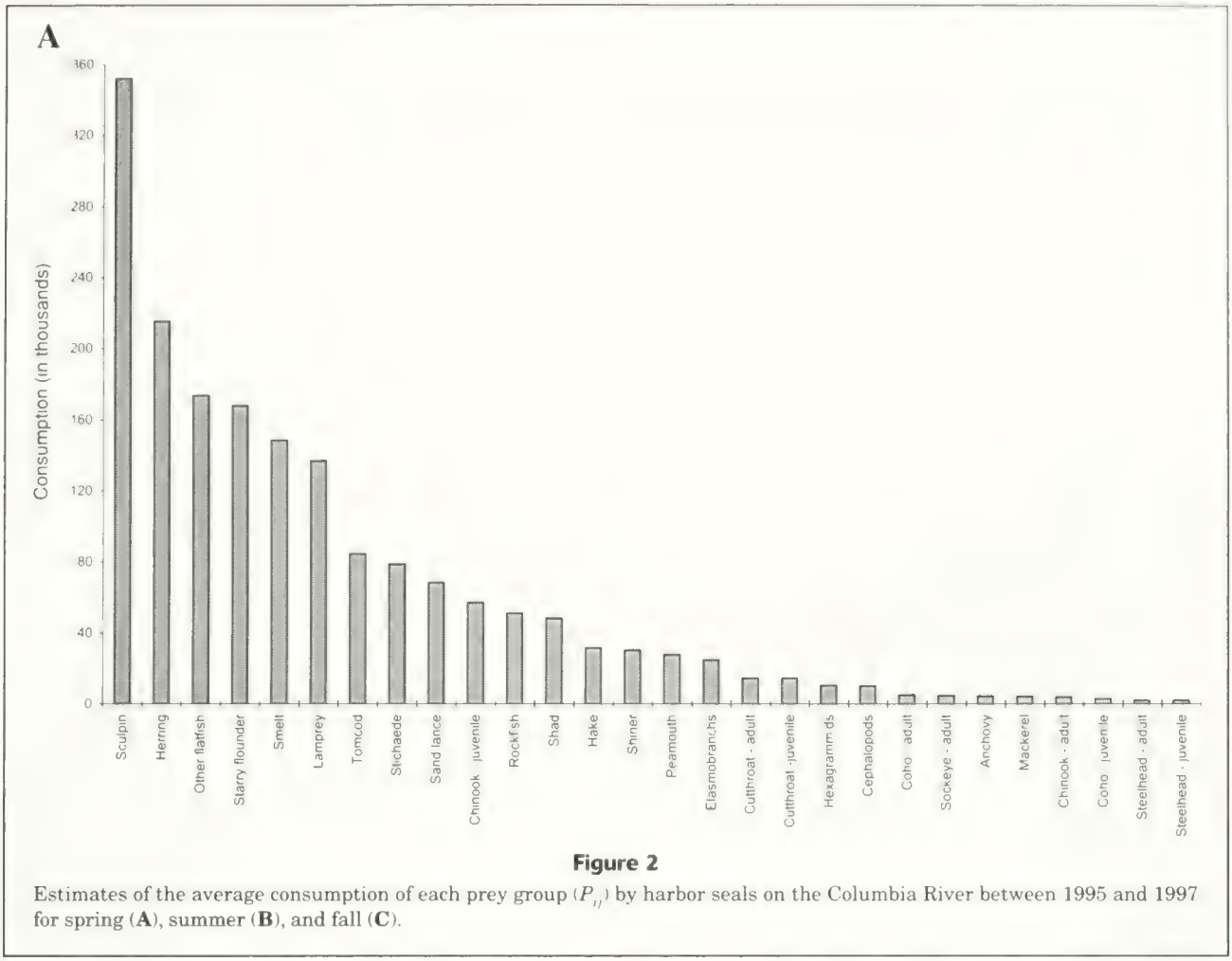


Figure 2

Estimates of the average consumption of each prey group (P_{ij}) by harbor seals on the Columbia River between 1995 and 1997 for spring (**A**), summer (**B**), and fall (**C**).

prey items weighing 10–20 g, SSFO predicted consumption that was 10 times greater than BR. Likewise, for prey items with a 1 kg mass or greater, SSFO predicted consumption estimates that were less than one-tenth of the BR estimate. For prey items near the median mass of 173 g, both estimators produced similar results.

Discussion

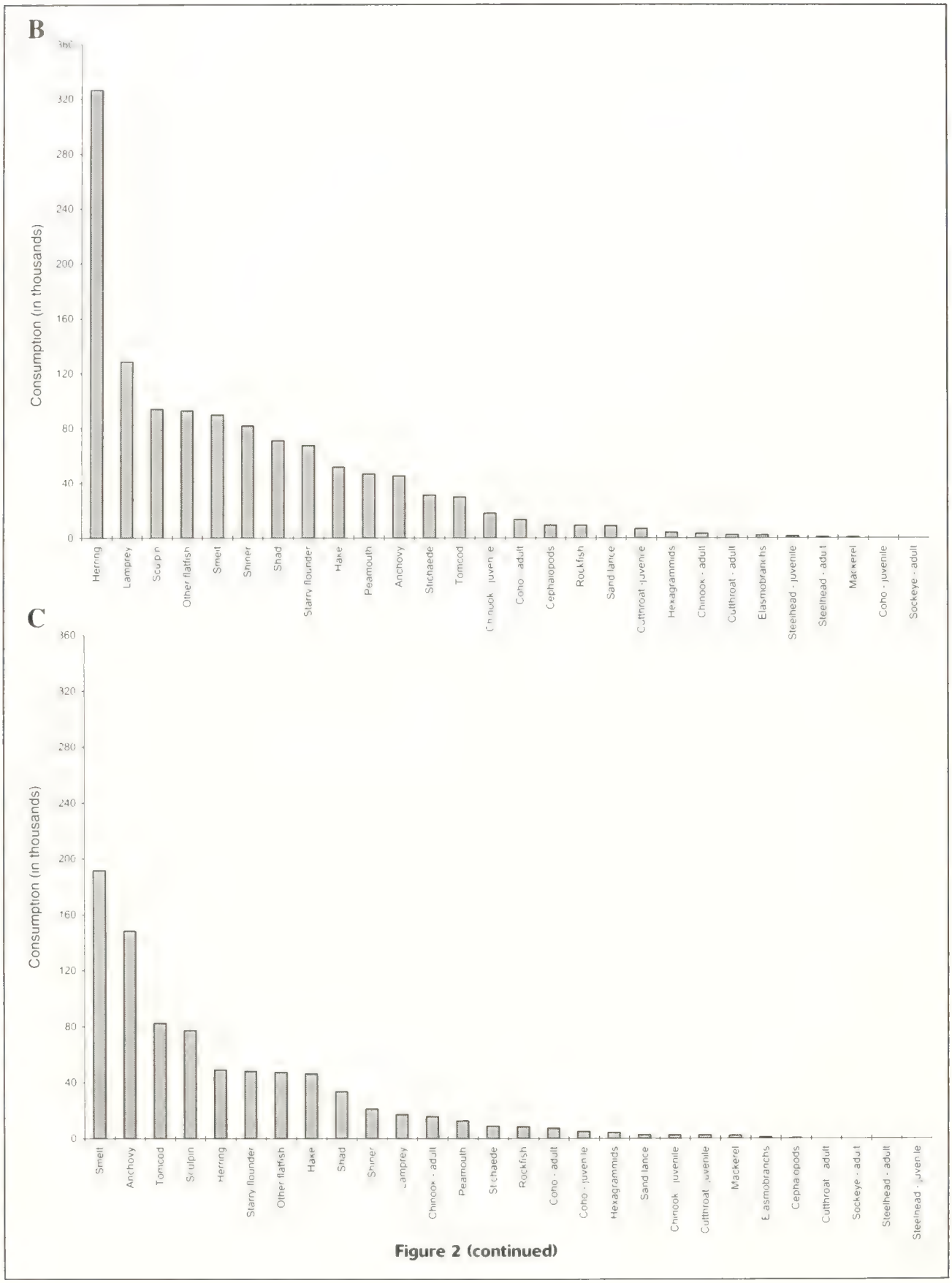
The consumption estimates for the Columbia River harbor seals could be improved by incorporating differences in energy density across prey and by measuring the sex- and age-structure of the seal population through time rather than using a life-table which may not be appropriate. These are valid criticisms and they could be overcome by collecting additional data. However, we believe these are less important than the current inadequacies in measuring diet composition that will likely affect any study that attempts to estimate consumption based on scat analysis.

It is well recognized that digestion does not act equally on all hard parts and is certainly species-specific for otoliths (Harvey, 1989). We included other hard parts such as bone to reduce bias due to differential otolith digestion; however, that inclusion may not remove all of the selectivity bias and it certainly introduces several other problems discussed below. Also, because hard parts are used for diet composition, if seals are only eating the fleshy parts of large fish, a significant portion of their diet may be missed.

Table 4

Proportion of variance of the adult chinook consumption estimate resulting from each estimation component.

	Diet composition		Harbor seal	
Season	Year (σ_y)	Date (σ_t)	Biomass (σ_r)	Population size
Spring	0.00	0.14	0.82	0.04
Summer	0.00	0.51	0.44	0.04
Fall	0.20	0.16	0.59	0.05



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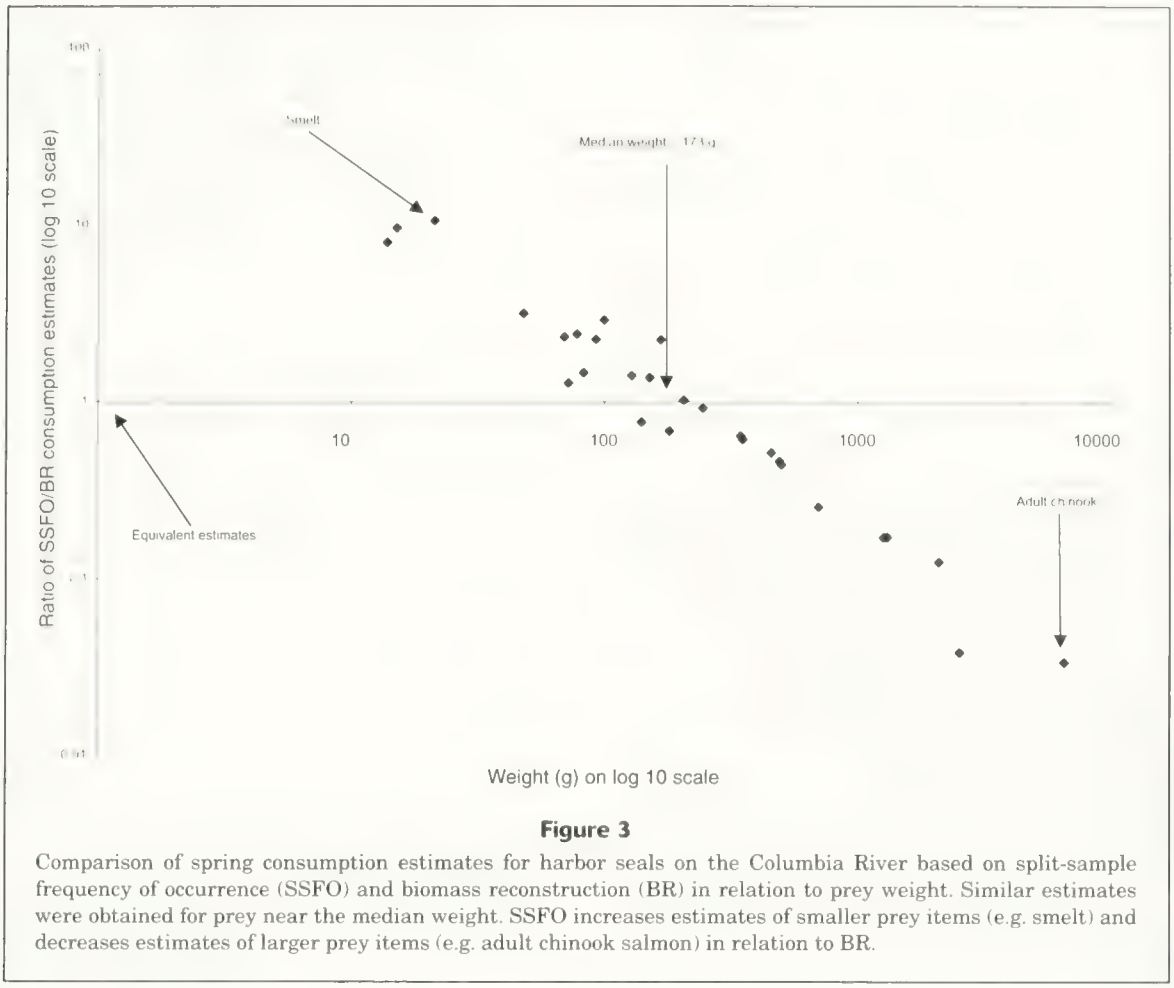

Figure 3

Comparison of spring consumption estimates for harbor seals on the Columbia River based on split-sample frequency of occurrence (SSFO) and biomass reconstruction (BR) in relation to prey weight. Similar estimates were obtained for prey near the median weight. SSFO increases estimates of smaller prey items (e.g. smelt) and decreases estimates of larger prey items (e.g. adult chinook salmon) in relation to BR.

We have assumed an equal probability of recovering identifiable skeletal remains from all prey sizes and that masses predicted from otolith measurements represent prey identified from other structures. There are several situations when recovered otoliths may not correctly represent the size of prey consumed. Small otoliths from small individuals of a species may be more likely to be completely digested. In that case, biomass would be overestimated because the larger otoliths would be recovered from larger fish. Also, otoliths may have different passage rates due to changes in their structure as fish age resulting in a size bias. Consumption estimates could thus be erroneously high or low because prey would be calculated from a single size group rather than the range of prey consumed. Unequal digestion may also create errors in estimated mass from the otoliths that are recovered. Our estimated mass may have been biased because we applied an average degradation factor to adjust otolith length. A better alternative would be to grade otolith condition and apply condition-specific degradation factors (Tollit et al., 1997b).

Counting the number of individual prey items is not possible with nonunique bones. Instead, we estimated a minimum number of individuals (MNI) contained in the scat (n_{ij}=MNI). MNI from all skeletal elements is a minimum estimate because the presence of many nonunique structures are assigned to a single prey item when they could represent several different prey. This error would not bias diet composition if it did not vary over species and size. However, differential passage of unique structures and identifiability among species result in the greater probability of detecting some prey (Browne et al., 2002). To minimize interspecific biases, we could use an MNI of 1 for all bones, regardless of the enumeration of unique structures for some species. While this would reduce some problems with species differences, it would exacerbate differences associated with prey size because large prey would be accurately reflected by an MNI of 1 and small prey that are eaten in greater quantities would be severely underestimated.

Bowen (2000) proposed estimating the number of prey consumed by correcting the otolith count with rates of otolith recovery from feeding trials. These correction factors vary widely between seals and studies and are influenced by a variety of factors, including size of individual prey, meal size, and activity of harbor seals (Harvey, 1989; Harvey and Antonelis, 1994; Cottrell et al., 1996; Tollit et al., 1997b). Browne et al. (2002) examined the ratio of otolith-

corrected estimates of MNI for several species. The ratios were quite variable but the comparison did suggest that smaller prey such as smelt were more likely to be underrepresented by using the minimum count.

If diet composition is based on sagittal otoliths, a fish can be represented by, at most, two scats and because all fish have two sagittal otoliths, fish size should not influence the probability that a particular fish is included, in a sample of scats, except through size-specific passage rates of otoliths. However, when all hard parts are included, the sampling may be size-biased if the size of the prey affects the number of scats in which the hard parts are deposited. Larger prey contain larger hard parts that may require longer passage times; therefore larger prey may be deposited in more scats than smaller prey. Also, large prey may be shared among seals as a result of cooperative feeding behavior and could be deposited in several scats. If either situation occurs, larger prey would be more likely to be included in the sample and would be over-represented. Because the scat is the sampling unit, any prey-size or species-specific effects on scat deposition rate may also bias diet composition estimators.

The effect of over-representing large prey depends on the estimator used for diet composition. The different outcomes with Equations 1–3 can be demonstrated with a simple example. Consider a sample of two scats in which one scat contains the remains of a 2-kg salmon and another scat contains the remains of ten 10-g anchovy and four 100-g herring. From Equation 1, the diet composition would be 80% (2000/2500) salmon, 4% anchovy, and 16% herring based on proportions of total reconstructed biomass. From Equation 2, we would estimate that salmon represent 50% of the diet from the two samples that are 100% and 0% salmon, and likewise 10% anchovy and 40% herring. Finally from Equation 3, we would estimate that the diet was 50% salmon, 25% anchovy, and 25% herring. If the small prey were undercounted in relation to the large salmon, the influence of the error influences the composition within the scat for Equations 2 and 3, but for BR (Eq. 1) the error extends across all samples.

As with the Columbia River harbor seal example (Fig. 3), the differences in the estimators are primarily the result of large prey in the weighted versus unweighted averages. Some difference would be expected in the results of Equations 2 and 3 depending on the validity of the equal volume assumption. SSFO (Eq. 3) simplifies the analysis of diet composition to a measure of presence and absence by assuming that prey within the same scat were consumed in equal volumes. The simplifying assumption removes the necessity to enumerate prey and measure mass from morphometric relationships with prey remains. However, the equal volume assumption does not seem particularly reasonable and its implementation is arbitrary, depending on how the prey are classified unless all prey remains can be identified to species. Olesiuk (1993) showed that the diet composition percentages for the primary prey varied by a factor of two or three, depending on the assumed composition within each scat. We expected that these differences would depend on the diversity of the diet. How closely they represented the true diet would depend on the range in prey sizes.

From our viewpoint, we do not see a clear choice between the estimators for diet composition. The use of consumption estimates from SSFO and BR to provide a range of estimates may have limited application in cases where each approach would suggest a similar conclusion. However, for large prey, such as salmonids, a tenfold difference in estimates, compounded with the uncertainty from sampling and biomass estimation, may yield too little information to develop a reliable conclusion about the impact of pinniped predation on salmonid stocks.

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Appendix

We have constructed variance estimators for diet composition and consumption rates using finite population sampling methods (Cochran, 1977) and delta method approximations based on the Taylor series (Seber, 1973). Variance estimates and confidence intervals could also be constructed by using bootstrap techniques similar to the work of Hammond and Rothery (1996).

To describe the variance estimators, we use the following subscripts: i for prey group, j for season, y for year, and t for collection occasion within year. A dropped subscript implies summation or averaging over that subscript (e.g. s_{jy} is the total number of scats collected in season j of year y—summed over occasions). We define the following notation which was not used in our article:

T_{jy} = number of scat collection occasions,
s_{jy} = number of scats collected during the occasion,
Y_j = number of years in which season j was sampled of a total of Y years.

We have assumed that scat collected on each occasion is a varying proportion of a fixed and unspecified amount of prey biomass consumed. Thus, we computed unweighted averages of the proportions over occasions and then over years:

$$\hat{\pi}_{ijy} = \frac{\sum_{t=1}^{T_{jy}} \hat{\pi}_{ijyt}}{T_{jy}} \qquad \hat{\pi}_{ij} = \frac{\sum_{y=1}^{Y_j} \hat{\pi}_{ijy}}{Y_j}.$$

We have also assumed that scat samples are independent which would be a concern in the unlikely event that the same seal deposited multiple scats at one time. We have also assumed that the collection occasions which are limited to low tides represent a random sample of dates within a season.

The variance of diet composition was based on multistage sampling scheme stratified by season (Cochran, 1977) that was composed of the following stages: estimation of biomass proportion consumed for each occasion, sampling of occasions within season of a year, and sampling of years. We have limited inference to the Y years that were sampled. Thus, if a season was sampled in each

year there is no annual variance component. The variance of the diet composition for a prey group for a single season is the sum of three components corresponding to the three stages: estimation of biomass proportion (σ_b^2), sampling of occasions (σ_t^2), and sampling of years (σ_y^2). Following Cochran (1977), the estimators for each component are

$$\hat{\sigma}_b^2 = \frac{\sum_{y=1}^{Y}\sum_{t=1}^{T_y} \widehat{Var}_b(\hat{\pi}_{ijyt})}{\sum_{y=1}^{Y} T_y},$$

$$\hat{\sigma}_t^2 = \frac{Y_j}{Y} \frac{\sum_{y=1}^{Y}\sum_{t=1}^{T} (\hat{\pi}_{ijyt} - \hat{\pi}_{ijy})^2}{\sum_{y=1}^{Y} T_y \sum_{y=1}^{Y} (T_{yj} - 1)},$$

$$\hat{\sigma}_y^2 = \frac{\left(1 - \frac{Y_j}{Y}\right)\sum_{y=1}^{Y} (\hat{\pi}_{ijy} - \hat{\pi}_{ij})^2}{Y_j(Y_j - 1)}.$$

We used the delta-method (Taylor series approximation) (Seber 1973) to estimate the variance of the estimated proportion for occasion t which expressed in matrix notation is

$$\widehat{Var}_b(\hat{\pi}_{ijyt}) = \widehat{Var}_b\left(\frac{\hat{b}_{ijyt}}{\sum_{r=1}^{\omega} \hat{b}_{rjyt}}\right) = \beta' \Sigma \beta,$$

where β is a vector of partial-derivatives of π_{ijyt} with respect to b_{rjyt} for r=1, ω and Σ is the $\omega \times \omega$ variance-covariance matrix of $\hat{b}_{rjyt}$ for r=1,ω. Likewise, the variance of ρ_{ij} was estimated by using

$$\widehat{Var}(\hat{\rho}_{ij}) = \left[\frac{\hat{\sigma}_y}{\overline{w}_{ij}}\right]^2 + \left[\frac{\hat{\sigma}_t}{\overline{w}_{ij}}\right]^2 + \hat{\sigma}_\rho^2,$$

where

$$\hat{\sigma}_\rho^2 = \frac{\sum_{y=1}^{Y}\sum_{t=1}^{T_y} \widehat{Var}_b(\hat{\rho}_{ijyt})}{\sum_{y=1}^{Y} T_y},$$

and

$$\widehat{Var}_b(\hat{\rho}_{ijyt}) = \widehat{Var}_b\left(\frac{\hat{n}_{ijyt}}{\sum_{r=1}^{\omega} \hat{b}_{rjyt}}\right) = \beta' \Sigma \beta,$$

where the elements in Σ and β for the i^{th} prey group are partitioned into $\hat{n}_{ijyt}$ and $\overline{w}_{ij}$. We also used the delta-method to obtain approximate variances and covariances in Σ of the biomass estimates for a single occasion

$$\widehat{Var}(\hat{b}_{ijyt}) = \hat{n}_{ijyt}^2 \hat{\sigma}_{\bar{w}}^2 + \hat{\sigma}_{\hat{n}}^2 \overline{w}_{ij}^2.$$

The first term in the variance is the uncertainty resulting from the variability in the estimate of the mean weight. For salmonid species, the second term measures the uncertainty resulting from apportioning the number of unknown salmonids into prey groups (i.e. estimating n_{ijyt}). For nonsalmonid species, all hard parts were classified into less specific prey groups; therefore $\hat{\sigma}_{\hat{n}} = 0$. The group-specific estimates of biomass within season are uncorrelated except for the estimates for salmonid species ($i \varepsilon \Psi$) which are correlated because of the apportionment of the items which were identified as salmonid but could not be identified to species nor to the juvenile and adult sizes. For salmonid groups r and $v \varepsilon \Psi$, the estimated covariance is

$$\widehat{Cov}(\hat{b}_{rjyt}, \hat{b}_{vjyt}) = \widehat{Cov}(\hat{n}_{rjyt}, \hat{n}_{vjyt}) \overline{w}_{rj} \overline{w}_{vj}.$$

The total amount of biomass represented by the scats is the sum across all prey groups:

$$\hat{b}_{jyt} = \sum_{i=1}^{\omega} \hat{b}_{ijyt},$$

and its variance was estimated as

$$\widehat{Var}(\hat{b}_{jyt}) = \sum_{i=1}^{\omega} \widehat{var}(\hat{b}_{ijyt}) + 2 \sum_{r \varepsilon \psi} \sum_{v > r, v \varepsilon \psi} \widehat{cov}(\hat{b}_{rjyt}, \hat{b}_{vjyt}).$$

The variance of n_{ijyt} was estimated assuming a binomial distribution:

$$\widehat{Var}(\hat{n}_{ijyt}) = \sigma_n^2 = u_{jyt}^2 \frac{\hat{\gamma}_{ij}(1 - \hat{\gamma}_{ij})}{o_{ij}},$$

and the covariance between salmonid groups was estimated as

$$\widehat{Cov}(\hat{n}_{rjyt}, \hat{n}_{vjyt}) = -u_{jyt}^2 \frac{\hat{\gamma}_{rj} \hat{\gamma}_{vj}}{o_{ij}}.$$

We assumed that the weights of the prey consumed were independent samples from a group- and season-specific distribution with mean μ_{ij}, and variance σ_{ij}^2. The parameters μ_{ij} and σ_{ij}^2 were estimated with the predicted weights from the sample of o_{ij}^* measurable hard parts:

$$\hat{\mu}_{ij} = \overline{w}_{ij} = \frac{\sum_{u=1}^{o'} \hat{w}_{ijyu}}{o_{ij}^*} \quad \text{and} \quad \hat{\sigma}_{ij}^2 = \frac{\sum_{u=1}^{o'} (\hat{w}_{ijyu} - \overline{w}_{ij})^2}{o_{ij}' - 1}.$$

To incorporate uncertainty in regression parameters and prediction error for the measured hard parts and variability in mass for the unmeasured prey ($n_{ij} - o_{ij}^*$), the variance of μ_{ij} should be estimated by

$$\widehat{Var}(\hat{w}_{ij}) \approx \hat{\sigma}_{ij}^2 \frac{\sum_{u=1}^{o_{ij}^*} \widehat{Var}(\hat{w}_{ijku})}{o_{ij}^{*2}} + \left(\frac{n_{ij} - o_{ij}^*}{n_{ij}}\right)\frac{\hat{\sigma}_{ij}^2}{o_{ij}^*},$$

where the variance of $\hat{w}_{ijku}$ is the prediction variance for the u^{th} otolith. When these data were analyzed, the available regression equations in a draft version of Harvey et al. (2000) did not include standard errors for the parameters nor the residual variance that were needed to compute the prediction variance. Therefore, unfortunately we had to drop the first term from the variance. The necessary values are now available in Harvey et al. (2000). The second-term measures variability between prey and is typically larger than the prediction error. However, to avoid underestimating this component of variance we dropped the finite population correction (fpc) factor on the second term. If we had used the fpc for salmonids, we would have had to replace the unknown n_{ij} with their estimated values.

For variance estimates of number of prey consumed (P_{ij}) we also used a delta method approximation:

$$\widehat{Var}(\hat{P}_{ij}) \approx \hat{P}_{ij}^2\left[cv^2(\xi_j) + cv^2(\hat{\rho}_{ij})\right].$$

We did not have variance estimates for energetic requirements nor age structure; therefore the variation in estimated prey biomass requirement (ξ_j) reflected only variation in our estimates of population size:

$$cv(\xi_j) = cv(\hat{N}_j) \approx \sqrt{cv^2(\bar{c}_j) + cv^2(f)},$$

which was also approximated by the delta method.

Vertical and horizontal movements of southern bluefin tuna (*Thunnus maccoyii*) in the Great Australian Bight observed with ultrasonic telemetry

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Abstract—The vertical and horizontal movements of southern bluefin tuna (SBT), *Thunnus maccoyii*, in the Great Australian Bight were investigated by ultrasonic telemetry. Between 1992 and 1994, sixteen tuna were tracked for up to 49 h with depth or combined temperature-depth transmitting tags. The average swimming speeds (measured over the ground) over entire tracks ranged from 0.5 to 1.4 m/s or 0.5 to 1.4 body lengths/s. The highest sustained swimming speed recorded was 2.5 m/s for 18 hours. Horizontal movements were often associated with topographical features such as lumps, reefs, islands and the shelf break. They spent long periods of time at the surface during the day (nearly 30%), which would facilitate abundance estimation by aerial survey. At night, they tended to remain just below the surface, but many remained in the upper 10 m throughout the night. SBT were often observed at the thermocline interface or at the surface while travelling. A characteristic feature of many tracks was sudden dives before dawn and after sunset during twilight, followed by a gradual return to their original depth. It is suggested that this is a behavior evolved to locate the scattering layer and its associated prey when SBT are in waters of sufficient depth. SBT maintained a difference between stomach and ambient temperature of up to 9°C.

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Southern bluefin tuna, *Thunnus maccoyii*, spawn in the northeast Indian Ocean south of the Sunda Islands from August to May (Farley and Davis, 1998). Young-of-the-year move down the west coast of Australia and first appear in the Great Australian Bight as 1-year olds. They aggregate in the Bight during the Austral summer, disperse to the east or west within latitudes of 30–40°S in autumn, and return to the Bight in spring. Juveniles between 1 and 4 years old return each summer to the Bight where they form extensive surface schools.

To provide a fishery-independent index of recruitment, line transect aerial surveys have been flown in the Bight each summer since 1990 to estimate the relative abundance of juveniles visible in the top 5 m (Chen et al.[1]). The largest source of variance in these estimates is thought to be environmental factors that influence both surfacing behavior and aerial detection. To investigate these problems, we used ultrasonic telemetry to provide the first information on surfacing behavior and short-term horizontal and vertical movement patterns that might influence sightings from the air. More comprehensive information on tuna surfacing for the whole of the three-month survey period is expected from an archival tagging program begun in 1992 (Gunn et al.[2]). Because these data are dependent upon the recapture of archival-tagged fish, this information will not be available for some time.

Because of Carey's pioneering work on Atlantic bluefin tuna (Carey and Lawson, 1973), ultrasonic telemetry has been used to study many tuna species, including Atlantic (Lutcavage et al., 2000) and Pacific bluefin tuna (Marcinek et al., 2001), yellowfin tuna (Carey and Olsen, 1982; Cayré and Chabanne, 1986; Yonemori, 1982; Holland et al., 1990a; Cayré, 1991; Cayré and Marsac, 1993; Block et al., 1997; Brill et al., 1999; Marsac et al.[3]), skipjack tuna (Yuen, 1970; Dizon et al., 1978; Levenez, 1982; Cayré and Chabanne, 1986; Cayré, 1991), bigeye tuna (Holland et al., 1990a, 1992; Holland and Sibert, 1994), and albacore (Laurs et al., 1977). A number of small (35–46 cm) southern bluefin tuna (SBT) have been tracked in the Indian Ocean off

[1] Chen, S., A. Cowling, and T. Polacheck. 1995. Data analysis of the aerial surveys (1991–1995) for juvenile southern bluefin tuna in the Great Australian Bight. 1995 Southern Bluefin Tuna Recruitment Monitoring Workshop Report RMWS/95/6, 57 p. CSIRO Marine Laboratories, Castray Esplanade, Hobart, Tasmania, Australia 7000.

[2] Gunn, J., T. Davis, T., Polacheck, A. Betlehem, and M. Sherlock. 1995. The application of archival tags to study SBT migration, behaviour and physiology. Progress Report—1994–95. Southern bluefin tuna recruitment monitoring and tagging program workshop, 7–10 August 1995, Hobart, Australia. Rep. RMWS/95/8, 17 p. CSIRO Marine Laboratories, Castray Esplanade, Hobart, Tasmania, Australia 7000.

[3] Marsac, F., P. Cayré, and F. Conand. 1995. Analysis of small scale movements of yellowfin tuna around FADs using sonic tagging. Expert Consultation on Indian Ocean tunas. 6th session. Colombo, Sri Lanka, 25–29 September 1995. Rep. TWS/95/2/10, 20 p. ORSTROM, Seychelles Fishing Authority, BP 570, Victoria, Mahé, Seychelles.

Western Australia (Fishery Agency of Japan[4,5]). All SBT in the current study were released and tracked in shelf waters, except for one fish that moved from the shelf into slope waters.

Methods

Tracking experiments on SBT were carried out in the Great Australian Bight over three years. In 1992, the tracking system was tested on a short cruise late in the fishing season and close to Port Lincoln. In 1993, the strategy was to obtain extended tracks of up to 48 hours to investigate day and night patterns in depth distribution and horizontal movement within the Great Australian Bight. In 1994, we planned short tracks to maximize the number of individual fish observed during daytime, so that their behavior could be linked to sightings by aerial survey carried out at the same time.

All SBT were caught by pole and line, except for tuna no. 7 (referred to simply as "tuna 7") which was caught on light game fishing tackle, and tuna 9, which swallowed the tag while free-swimming. The tuna were landed on a wet, plastic-covered, foam mat. The head was covered with a wet cloth, length of fish was measured, the tag attached or inserted, and the fish was released back into the school.

V16 (16 mm diameter) sonic tags (VEMCO, Halifax, Nova Scotia, Canada) of various frequencies (50–69 kHz), equipped with pressure sensors, were deployed on two fish in April 1992 and four fish in January and March 1993 (Table 1). Five of these tags were attached externally, behind the second dorsal fin of the tuna, by using the attachment technique described in Holland et al. (1985). The sixth was placed in the stomach with an oesophageal catheter.

V22 (22 mm diameter) tags transmitting on 40 kHz were used on ten tuna tracked in January and February 1994. These tags, which have stronger signals and lower transmission frequencies, have a much larger detection range than V16 tags. They also have the capacity for

Table 1

Release and tracking details of southern bluefin tuna tracked in the Great Australian Bight during the years 1992–94.

Tuna no.	Tag type	Date of release	Location	Length (cm)	Tag position	Duration of track (h)	Distance moved (km)	Mean speed		Cause of termination
								m/s	FL/s	
1	V16-P	29 Apr 1992	Cabbage Patch	90	external	12	34	0.79	0.87	weather
2	V16-P	30 Apr 1992	Cabbage Patch	90	external	18	48	0.74	0.83	poor signal
3	V16-P	27 Jan 1993	28 km W of Ward Island	94	external	49	175	0.99	1.06	voluntary
4	V16-P	30 Jan 1993	Ward Island	96	external	48	143	0.83	0.86	voluntary
5	V16-P	13 Mar 1993	Rocky Island	103	external	5	9	0.52	0.51	lost
6	V16-P	14 Mar 1993	Rocky Island	98	stomach	26	131	1.40	1.42	weather
7	V22-P	10 Jan 1994	7 km S of Cannan Reef	67	stomach	30	91	0.84	1.26	voluntary
8	V22-P	12 Jan 1994	7 km S of Cannan Reef	100	stomach	10	32	0.90	0.90	voluntary
9	V22-P	15 Jan 1994	Nuyts Reef	85	mouth	5	15	0.85	1.00	tag detached
10	V22-PT	16 Jan 1994	11 km SE of St Francis Island	92	stomach	13	40	0.85	0.93	tag regurgitated
11	V22-PT	17 Jan 1994	41 km W of Sceale Bay	114	stomach	13	46	0.98	0.86	tag regurgitated
12	V22-P	18 Jan 1994	41 km W of Sceale Bay	85	stomach	13	34	0.72	0.85	voluntary
13	V22-PT	19 Jan 1994	15 km W of Labatt Pt.	100	stomach	20	67	0.94	0.94	voluntary
14	V22-P	31 Jan 1994	41 km E of Sceale Bay	100	stomach	9	36	1.10	1.10	voluntary
15	V22-P	1 Feb 1994	7km S of Cannan Reef	102	stomach	1	2	0.64	0.63	fish lost
16	V22-P	2 Feb 1994	7km S of Cannan Reef	97	stomach	5	14	0.79	0.82	tag regurgitated

[4] Fishery Agency of Japan. 1990. Report of 1988 research cruise of the R/V *Shoyo-Maru*. Distribution of juvenile southern bluefin tuna off west coast of Australia, December 1988–January 1989. Rep. Res. Dep., Fish. Agency Jpn. 63:1–125. Pelagic Fish Resource Division, 5-7-1 Orido, Shimizu, Shizuoka 424, Japan.

[5] Fishery Agency of Japan. 1992. Report of 1989 research cruise of the R/V *Shoyo-Maru*. Distribution of juvenile southern bluefin tuna off west coast of Australia, September–December 1989. Rep. Res. Dep., Fish. Agency Jpn. 64:1–166. Pelagic Fish Resource Division, 5-7-1 Orido, Shimizu, Shizuoka 424, Japan.

dual channels enabling sequential transmission of pressure and temperature. Seven pressure tags and three pressure-temperature tags were deployed. All, except one, were inserted into the stomach. To retard regurgitation, two small hooks were tied to each tag with VICRYL dissolving sutures before being placed in the stomach. One tuna struck a tag with hooks during a calibration experiment, resulting in the tag attaching without the tuna leaving the water. This fish was tracked for five hours until the tag detached.

Standard tracking techniques were used (see Holland et al., 1985). The tracking equipment, including the remote-controlled hydrophone rotator, is described in Pepperell and Davis (1999). We attempted to track the fish at a distance of about 400 m, which we judged from signal strength, using distance and signal-strength calibrations carried out before tracking. The decoded data from single-channel tags were logged together with global positioning system (GPS) latitude and longitude, nominally at 1-second intervals, on a computer with VEMCO VSCAN/GPS software (Vemco, 1992). Temperature and depth data from dual-channel transmitters were logged at about 3-second intervals.

Conductivity-temperature-depth profiles were taken at the start and finish, and at convenient times during each track, with a digital data loggers international profiler. Additional information collected during each track included bottom depth, air temperature, wind speed, cloud cover (1–8 sectors covered), brightness (1–4), and presence of surface and subsurface schools of SBT. In 1994, we also recorded the depth distributions of SBT schools detected on the echosounder under the tracking vessel.

The tracking data were processed using a filtering program to delete spurious data, interpolate missing data, and generate data files at nominated time intervals. The program compared each depth with the seven previous data points (which were nominally recorded at 1-second and 3-second intervals for single- and dual-channel tags, respectively) and then deleted spurious records based on expected maximum and minimum depths and maximum depth-change rates. Similarly, a temperature filter deleted spurious values based on expected maximum and minimum temperatures and maximum temperature-change rates in data from the dual-channel transmitters. Complete vertical tracks were plotted against time with 20-second interval data. The position and sustained swimming speeds of tracked tuna were assumed to be the same as that of the tracking vessel. By using GPS data, speed was calculated over the ground from the straight-line distance travelled between points in 10 minutes. Vertical movements and horizontal movements in relation to the vessel were not considered. An attempt was made to match both the heading and speed of the tracked tuna so that the vessel reflected the movements of the fish.

Depth distribution of tuna was examined from 20-second interval data aggregated in 5-m depth bins stratified by day and night. The number of observations in each depth bin was then expressed as a proportion of the total number of observations in each day–night stratum. The speed distribution of tuna was examined from 10-minute interval data aggregated in 0.1 m/s bins stratified by day and night.

Results

The tracking system was developed for use on a variety of commercial vessels. In April–May 1992, five fish were released and two were tracked successfully (Table 1). Modifications were then made to the system and different transmission frequencies were selected to reduce interference. The improved system was used on two cruises in January and March 1993. Four fish were tracked for periods of up to 49 h (Table 1).

In 1994, tracking was carried out farther west because fish schools were not sighted farther east (Fig. 1), probably due to warm water remaining in the northwest section of the study area (Fig. 2). The whole period (8 January–3 February) was characterized by windy conditions that made catching and tracking fish difficult. Ten SBT were released with tags (Table 1). The longest track was 31 h, but some tracks were short because the fish regurgitated their tags. Other tracks were terminated voluntarily after sunset to maximize the number of daytime observations on different fish.

Tuna 1 was released SW of Liguana Island on 29 April 1992 at 0855 h (Figs. 1 and 2A). It headed WSW towards the shelf edge until tracking was terminated after 12 hours. Acoustic interference from the tracking vessel affected calculation of depth at certain vessel speeds, resulting in some gaps in the vertical data (Fig. 3A). During the day the fish spent most of its time at the surface, but frequently dived to near the bottom. Tuna schools spotted at the surface appeared to break up and then re-appear sometime later, more or less at the same rate that the tracked SBT moved in and out of the surface waters. The fish dived shortly after sunset and then returned to the mixed layer and oscillated around 30 m until tracking was terminated at 2108 h.

Tuna 2 was released SW of Liguana Island on 30 April 1992 at 1330 h (Fig. 1). The fish moved west throughout most of the track but slowed and changed direction many times from 0400 h. These direction changes occurred when the tuna reached cooler surface waters (Fig. 2A). It remained in the 17°C water, moving south along the boundary with the 16°C isotherm. Its vertical behavior can be seen in Figure 3B. Like tuna 1, this fish made a brief dive just after sunset.

Tuna 3 was released at The Lump, 28 km west of Ward Island on 27 January 1993 at 15:22 h and was tracked for 49 h (Figs. 1 and 2B). It moved into waters near the shelf edge, a movement matched by a conventionally tagged tuna that was released at 33°15′S, 133°49′E on 26 January 1993 and that was recovered five days later at 34°S, 132°17′E by a commercial fishing operation. The vertical behavior of tuna 3 is shown in Figure 4A. It spent considerable time near the surface in association with other tuna during the late afternoon on the first day. It seldom surfaced on the second day; neither did the other tuna. A commercial pole-and-line boat fishing in the same area

Figure 1

Geographic position of southern bluefin tuna tracks in the eastern Great Australian Bight. The number of each fish indicates the start of its track. Symbols along tracks represent hourly positions (open symbol=day, solid symbol=night).

on the second day could not chum fish to the surface; the fishermen had also observed many tuna at the surface the previous day.

Tuna 4 was released near Ward Island on 30 January at 16:40 h and was tracked for 48 hours. This fish remained within the general area of release until tracking was terminated (Figs. 1 and 2B). Vertical behavior is shown in Figure 4B. The fish was associated with surface schools until night on the first day. It was also associated with large numbers of tuna (observed on the echosounder) throughout the night. The surface activity of tuna schools was low throughout the next day. Tuna were observed on the echosounder at the same depth as the tracked tuna throughout the day and next night, but not in the same numbers as the day before.

Tuna 5 was released on 13 March 1993 at 11:50 h at Rocky Island (Fig. 1). It was tracked for about 4 hours before it was lost. At 1500 h the tracked fish, together with other tuna, followed a pole-and-line vessel that was chumming at the time and that had crossed our path. The fish was temporarily lost but was relocated an hour later, again following the chum line of the pole-and-line vessel.

Tuna 6 was released at Rocky Island on 14 March 1993 at 07:35 h and subsequently tracked for 26 h (Figs. 1 and 2C). At 08:15 h the tracked tuna was observed following the chum line of the pole-and-line vessel (Fig. 5B). It was associated with other tuna at or near the surface until about 11:00 h. At 12:00 h the fish moved rapidly offshore at about 2.5 m/s and was tracked to the shelf. On reaching the shelf break, it remained within a region of warmer

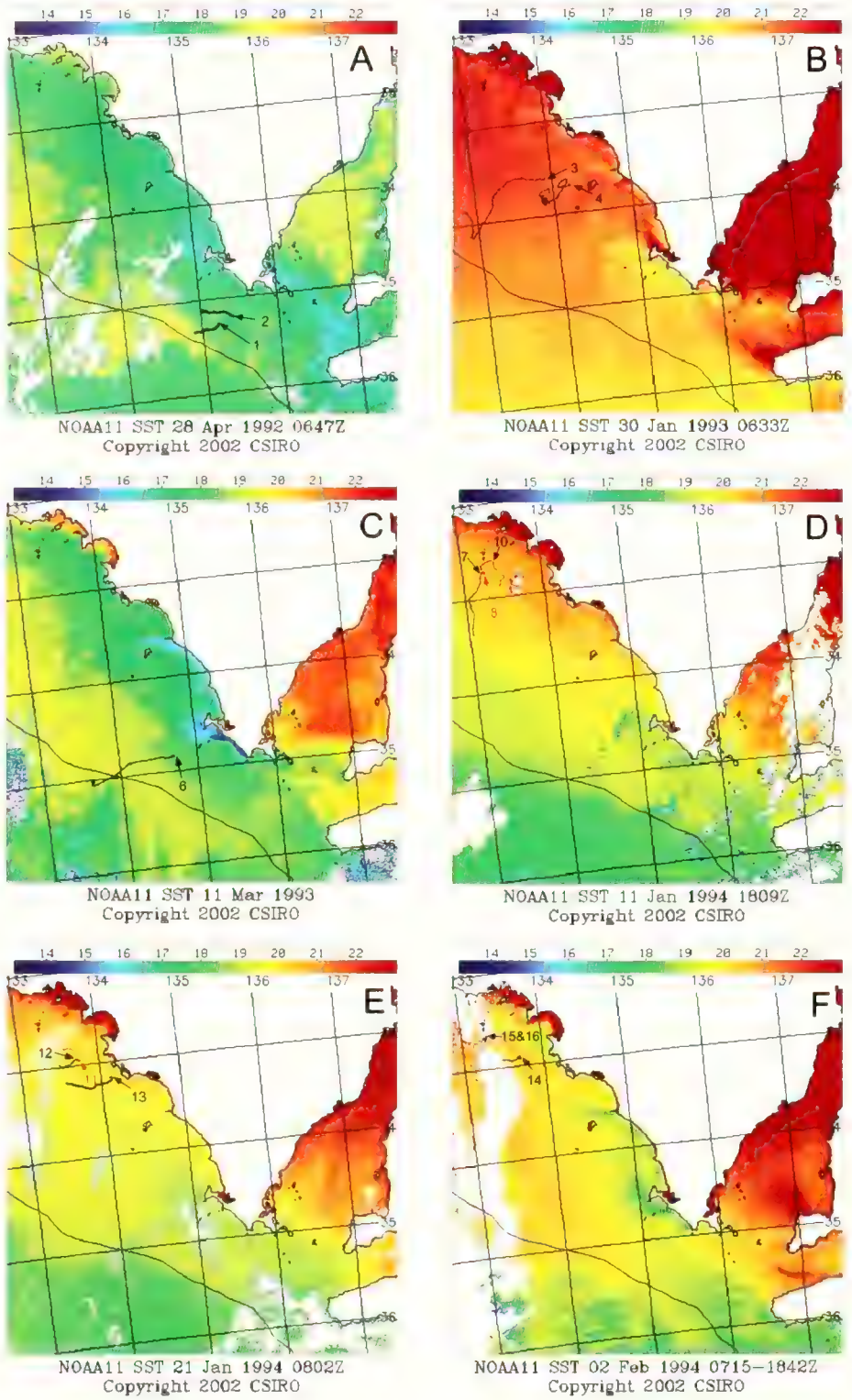

Figure 2

NOAA11 satellite sea-surface-temperature images of the study area during the periods of tracking with southern bluefin tuna tracks overlaid. (**A**) Tracks 1 and 2 on 29–30 April 1992. (**B**) Tracks 3 and 4 on 27–31 January 1993. (**C**) Track 6 on 14–15 March 1993. (**D**) Tracks 7, 8, and 10 on 10–16 January 1994. (**E**) Tracks 11–13 on 17–19 January 1994. (**F**) Tracks 14–16 on 31 January–2 February 1994.

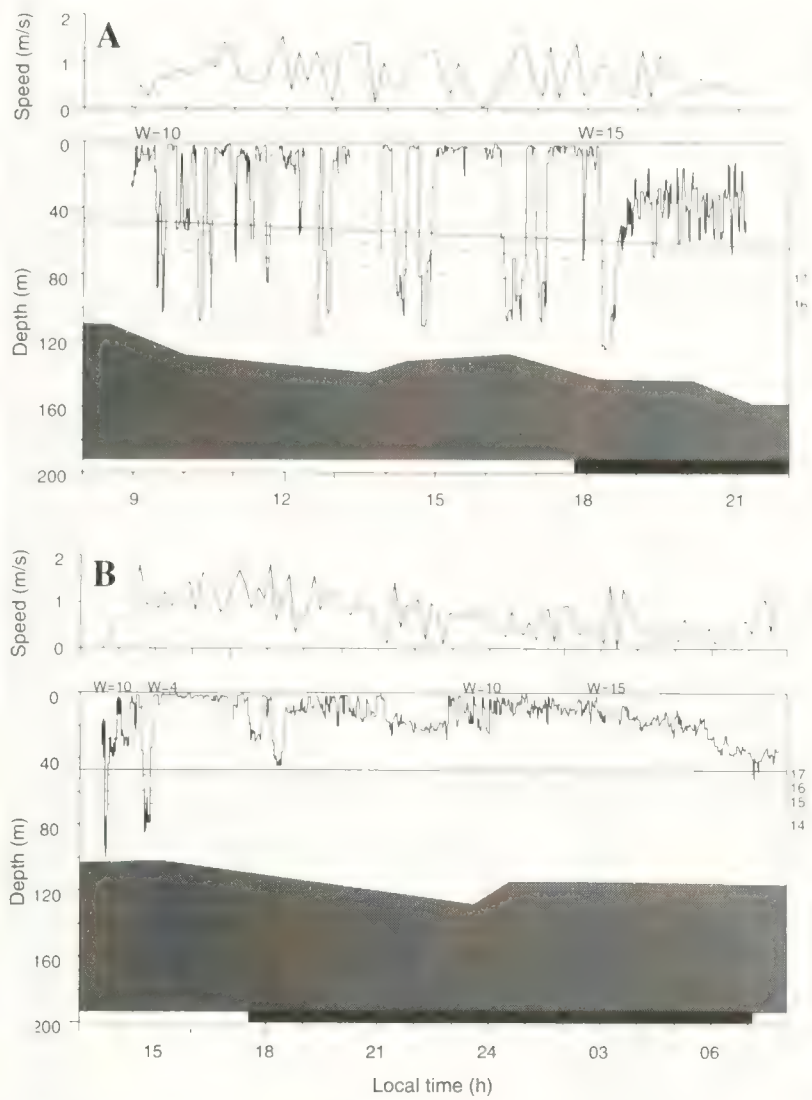

Figure 3

(**A**) Track of southern bluefin tuna 1 on 29 April 1992. (**B**) Track of southern bluefin tuna 2 on 30 April 1992. Speed over the ground (upper graph) and depth of the tuna (lower graph) are plotted against time. The sea bottom is indicated by shading, the solid line represents the bottom of the mixed layer and the dotted lines represent isotherms (°C). The black bar represents nighttime, the unshaded bar, daytime and W = wind speed in km/h.

surface water in association with a large subsurface school of tuna (Fig. 2C). While traveling to the shelf break, it remained near the bottom or just below the mixed layer. A deep sounding was made just after sunset and another just before dawn, the last reaching 180 m.

Tuna 7 was released at The Lumps 7 km south of Cannan Reef at 09:16 h on 10 January 1994 (Figs. 1 and 2D). This was the smallest fish tracked in this study. Unlike the others, it was caught on a trolled lure and landed after about a 5-minute struggle. Tracking was discontinued after 30 h due to bad weather. This fish was associated with large schools for the first five hours of tracking and again for three hours at first light the next day. It made postdusk and predawn dives (Fig. 6A).

Tuna 8 was released at The Lumps 7 km south of Cannan Reef at 10:58 h on 12 January 1994 (Figs. 1 and 2D). The fish was followed for 10 h until tracking was halted shortly after sunset. It remained in the upper 20 m for most of the track (Fig. 6B). At 12:50 h it followed the chum line of a pole-and-line vessel. From 14:00 to 16:00 h, it remained at the surface with a large school of tuna before slowing and sounding at a reef.

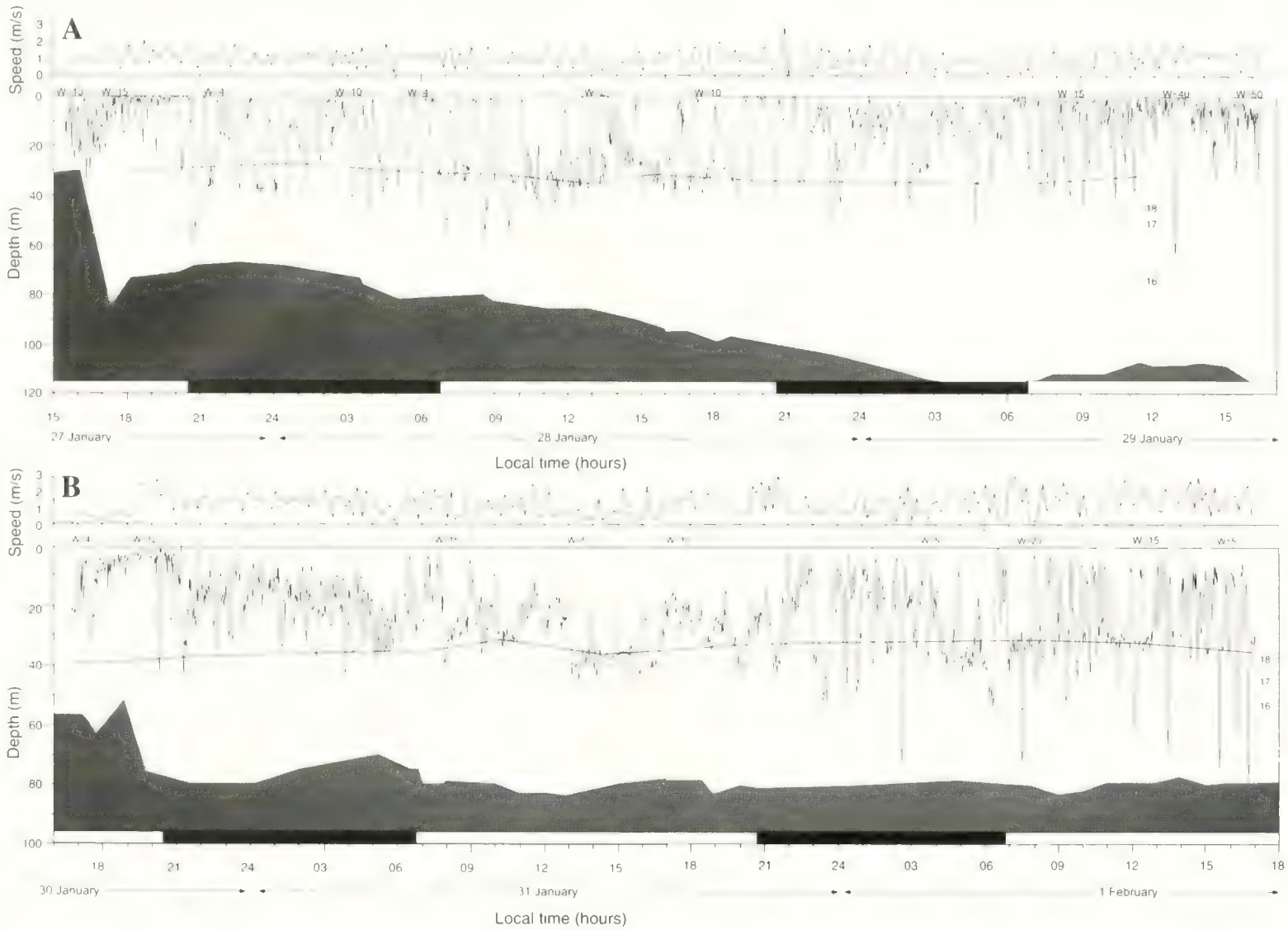

Figure 4

(**A**) Track of southern bluefin tuna 3 on 27–29 January 1993. (**B**) Track of southern bluefin tuna 4 on 30 January–February 1993. See Figure 3 for legend details.

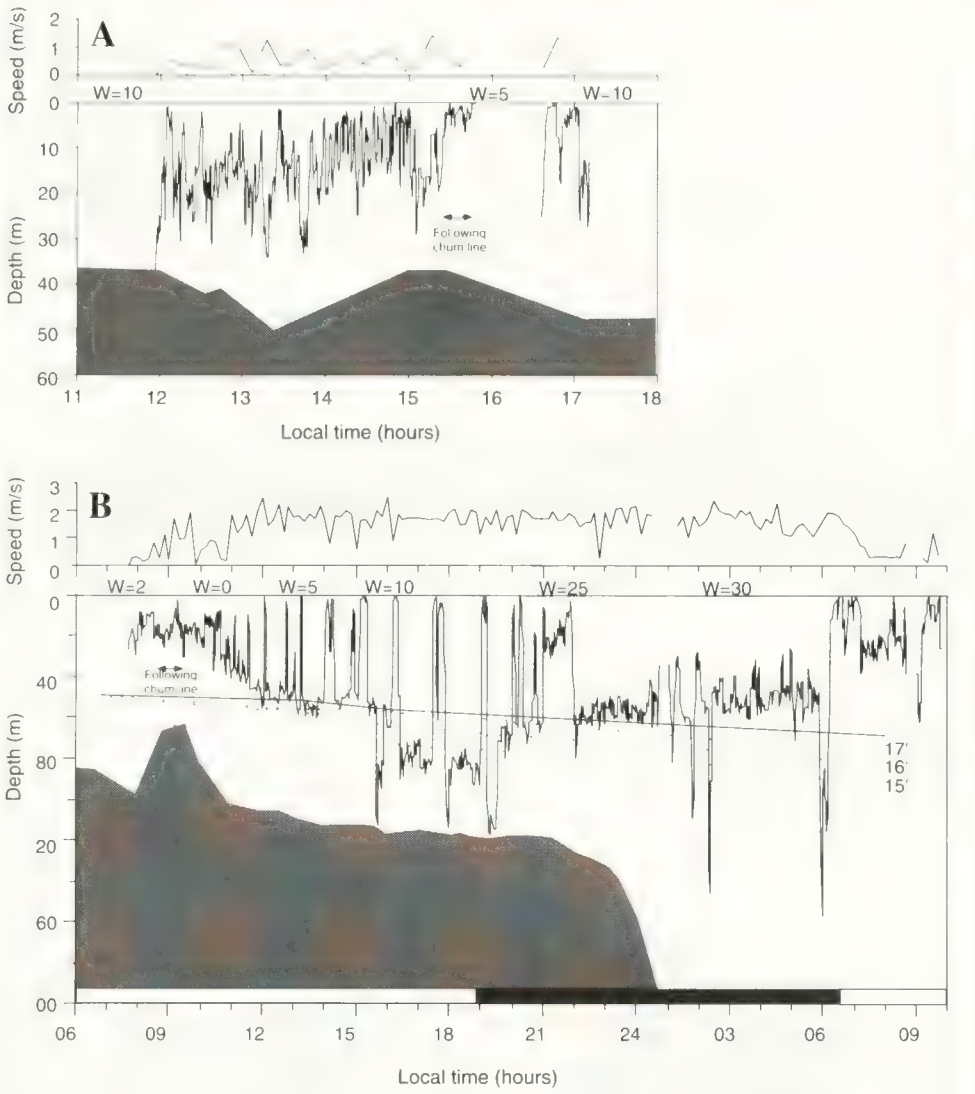

Figure 5

(**A**) Track of southern bluefin tuna 5 on 13 March 1993. (**B**) Track of southern bluefin tuna 6 on 14–15 March 1993. The period when the tuna followed the chum line is shown. See Figure 3 for legend details.

Tuna 9 struck at a tag during calibration experiments near Nuyts Reef at 09:05 on 15 January 1994 (Fig. 1). Consequently, it was tagged without leaving the water. The tag was either in the mouth or in the stomach. The tuna remained with tuna schools in the vicinity of tagging until 09:50 h and then moved away at considerable speed (2 m/s) for over an hour before sounding and slowing (Fig. 6C). It returned to the surface and remained there in association with a large surface school. The tag detached from the tuna at 1410 h.

Tuna 10 was released 11 km southeast of St Francis Island at 11:40 h on 16 January 1994. It was tracked for 13 h before it regurgitated the tag (Figs. 1 and 2D). The vertical movements of this fish differed from other tracks in that they were of relatively high amplitude (30+ m), traversed the water column, and were of moderate frequency (Fig. 7A). It spent little time at a particular depth, except for a short period at the bottom at the start of the track and again around 21:00 h. The fish was associated with tuna schools for most of the track. It made an extended dive just after sunset.

This was the first SBT to provide stomach-temperature data. The stomach temperature dropped rapidly initially, then increased to 25.4°C, which was about 6°C above water temperature. Temperature then decreased gradually for the rest of the track, but remained at least 4°C above ambient temperature.

Tuna 11 was released at The Lumps 41 km west of Sceale Bay at 13:57 h on 17 January 1994 with a temperature-pres-

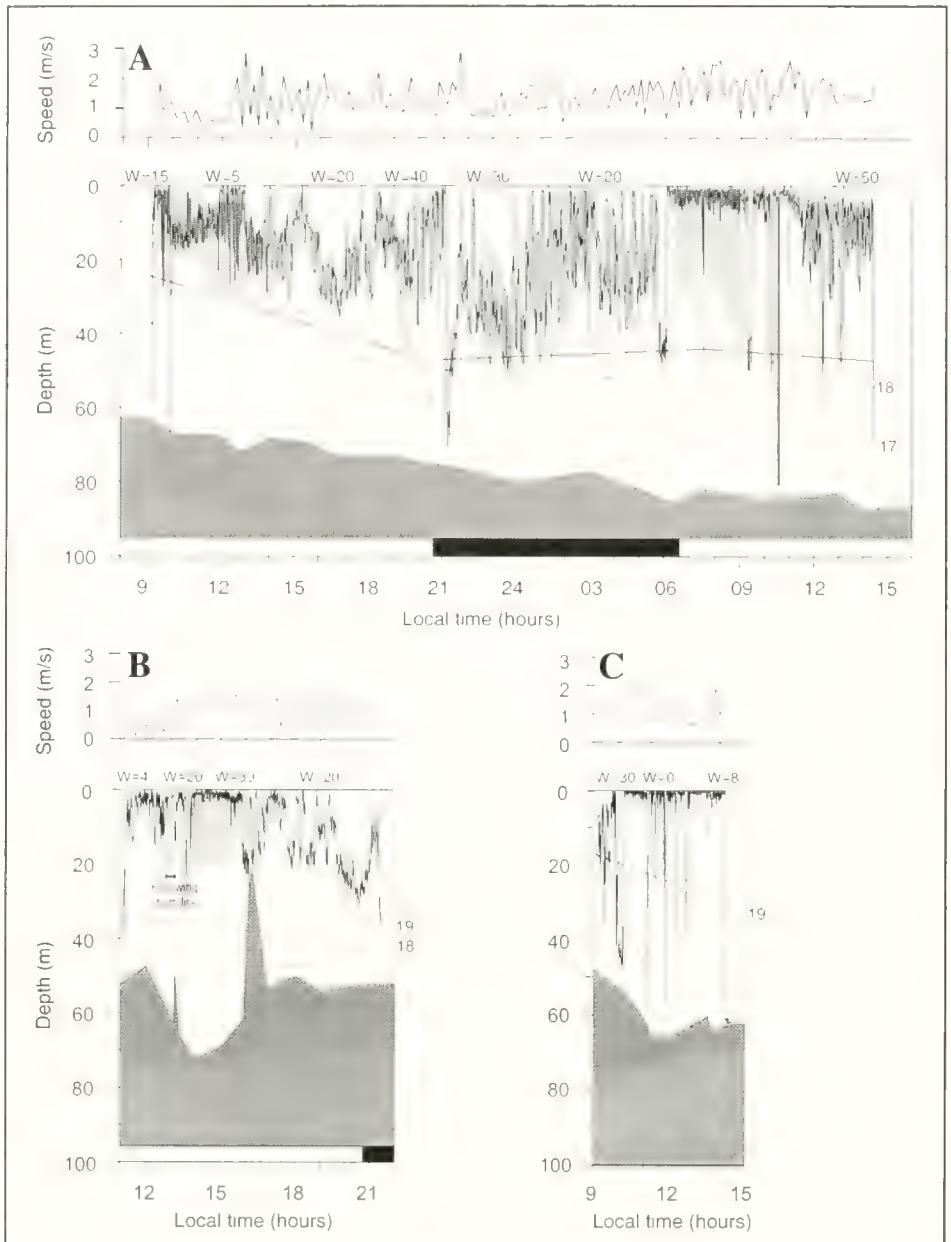

Figure 6

(**A**) Track of southern bluefin tuna 7 on 10–11 January 1994. (**B**) Track of southern bluefin tuna 8 on 12 January 1994. (**C**) Track of southern bluefin tuna 9 on 15 January 1994. Shading in the water column represents depth range of tuna schools detected by echosounder. See Figure 3 for other legend details.

sure tag in the stomach (Figs. 1 and 2E). This fish was associated with tuna schools for most of the track (Fig. 7B). Most vertical activity was oriented towards the surface, but periodic dives were made to or through the thermocline. At night the fish moved slightly deeper but continued to dive at regular intervals. It made an extended dive just after sunset.

The stomach temperature gradually increased through the night and by 01:00 h was at 28°C, which was 9°C above ambient temperature. At about 01:30 h there was a sudden drop in stomach temperature towards ambient temperature and then a gradual recovery that was most likely caused by the swallowing of prey or water (or both). The tag was regurgitated two hours later.

Tuna 12 was released at The Lumps 41 km west of Sceale Bay at 09:16 h on 18 January (Figs. 1 and 2E). It showed considerable vertical activity similar to tuna 10 and was associated with tuna schools throughout the track (Fig. 8A). It made an extended dive just after dusk.

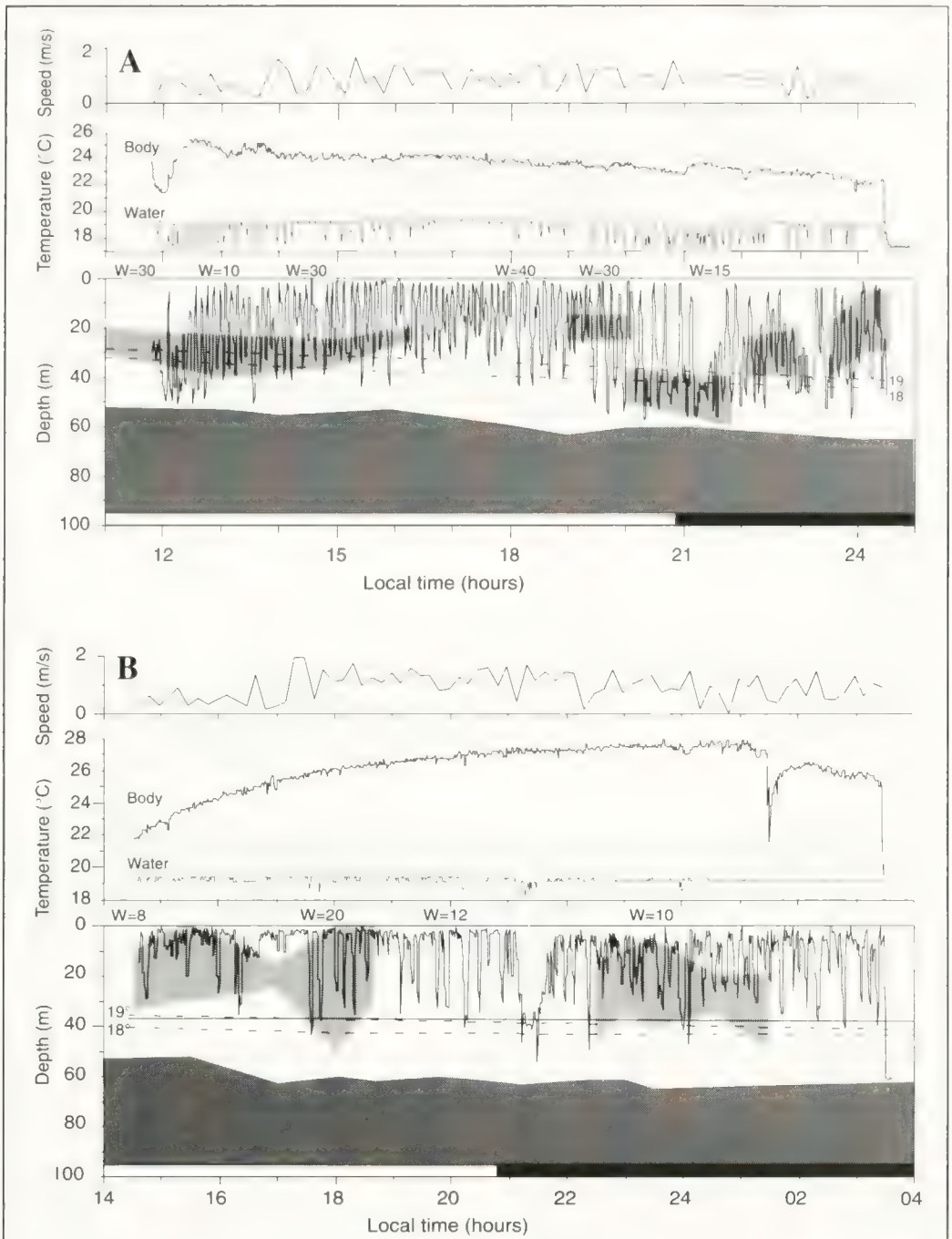

Figure 7

(**A**) Track southern bluefin tuna 10 on 16 January 1994. (**B**) Track of southern bluefin tuna 11 on 17–18 January 1994. See Figure 6 for legend details of upper and lower graphs. In the middle graph, stomach temperature and water temperature (interpolated from the depth of the fish and data logger temperature profiles) are plotted against time.

Tuna 13 was released 15 km west of Labatt Point at 1226 h on 19 January with a temperature-pressure tag in the stomach (Figs. 1 and 2E). This fish remained close to the surface during the day and deeper at the night, frequently staying just above the thermocline and sometimes diving through it. It made an extended dive after dusk and another just before dawn (Fig. 8B). It was associated with schools of tuna throughout the track. Although tuna schools did not appear on the echosounder during the afternoon, extensive bird activity and surface schools

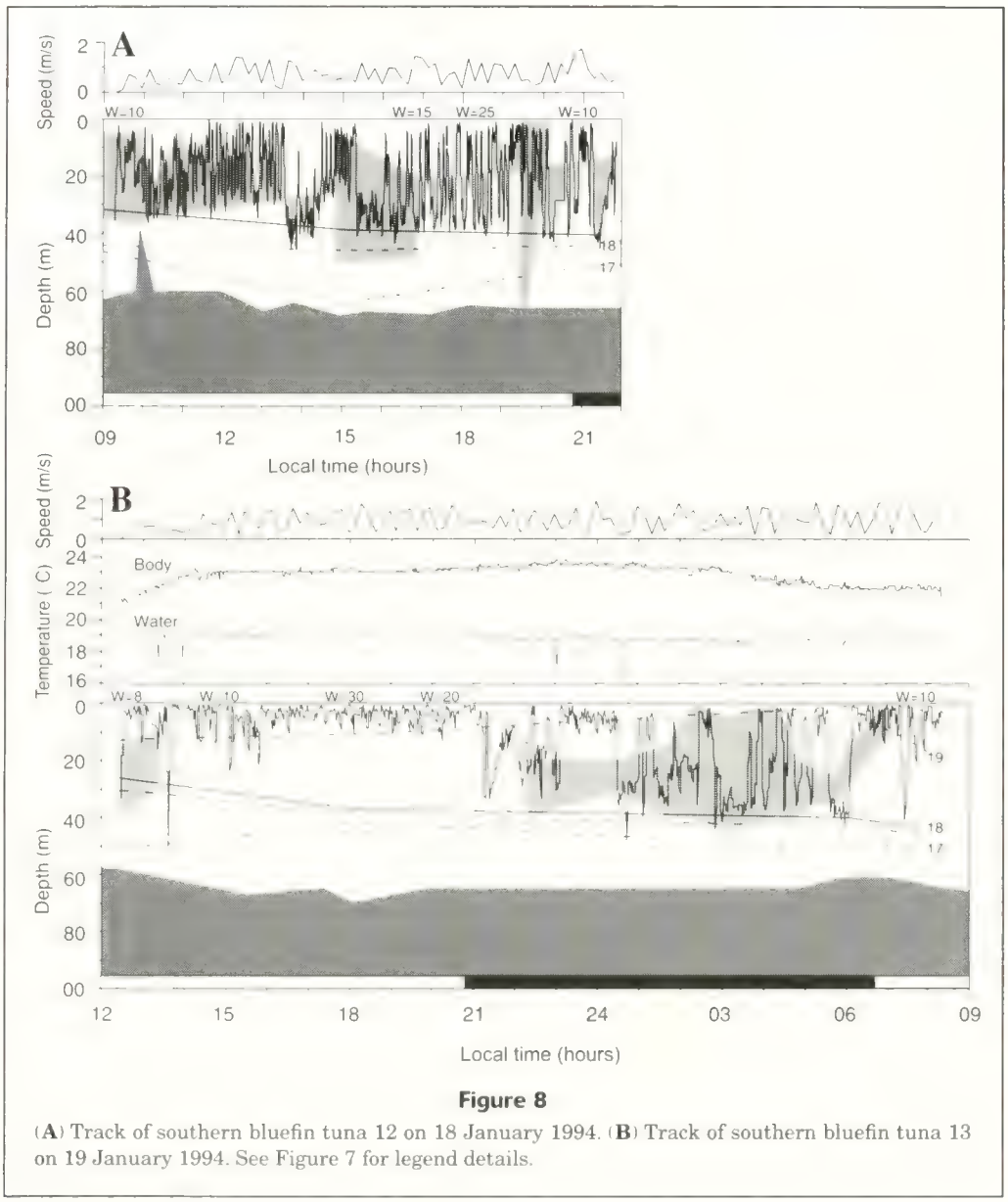

Figure 8

(**A**) Track of southern bluefin tuna 12 on 18 January 1994. (**B**) Track of southern bluefin tuna 13 on 19 January 1994. See Figure 7 for legend details.

of tuna were observed during the whole period that the tracked tuna was near the surface.

Stomach temperature showed a marked drop initially (presumably it swallowed water on its release) and then a gradual recovery. Temperature reached a peak of 23.8°C, about 4.5°C above ambient temperature, near midnight and then slowly declined throughout the remainder of the night.

Tuna 14 was released 41 km west of Sceale Bay at 12:26 h on 31 January 1994 (Figs. 1 and 2F). The tuna was lost for about 20 minutes early in the track (Fig. 9A). It had moved south before doubling back and returning to the reef where it had been tagged. At 16:40 h it then swam away with a school of tuna, remaining just above the thermocline and occasionally making excursions to the surface. It made an extended dive after dusk.

Tuna 15 was released at The Lumps 7 km south of Cannan Reef at 13:26 h on 1 February 1994 (Fig. 1). It joined a large school of tuna following the chum line of a pole-and-line vessel, but was lost one hour later.

Tuna 16 was released at The Lumps 7 km south of Cannan Reef at 09:30 h on 2 February 1994 (Figs. 1 and 2F). It was associated with schools initially, but they dispersed at about 1400 h (Fig. 9B). The tag was regurgitated at 15:20 h.

Time at depth

The proportion of time spent by tuna in 5-m interval depth strata was plotted by day and night for all tracks combined (Fig. 10). These data indicated that SBT are surface-oriented by day in the Great Australian Bight, spending a significant

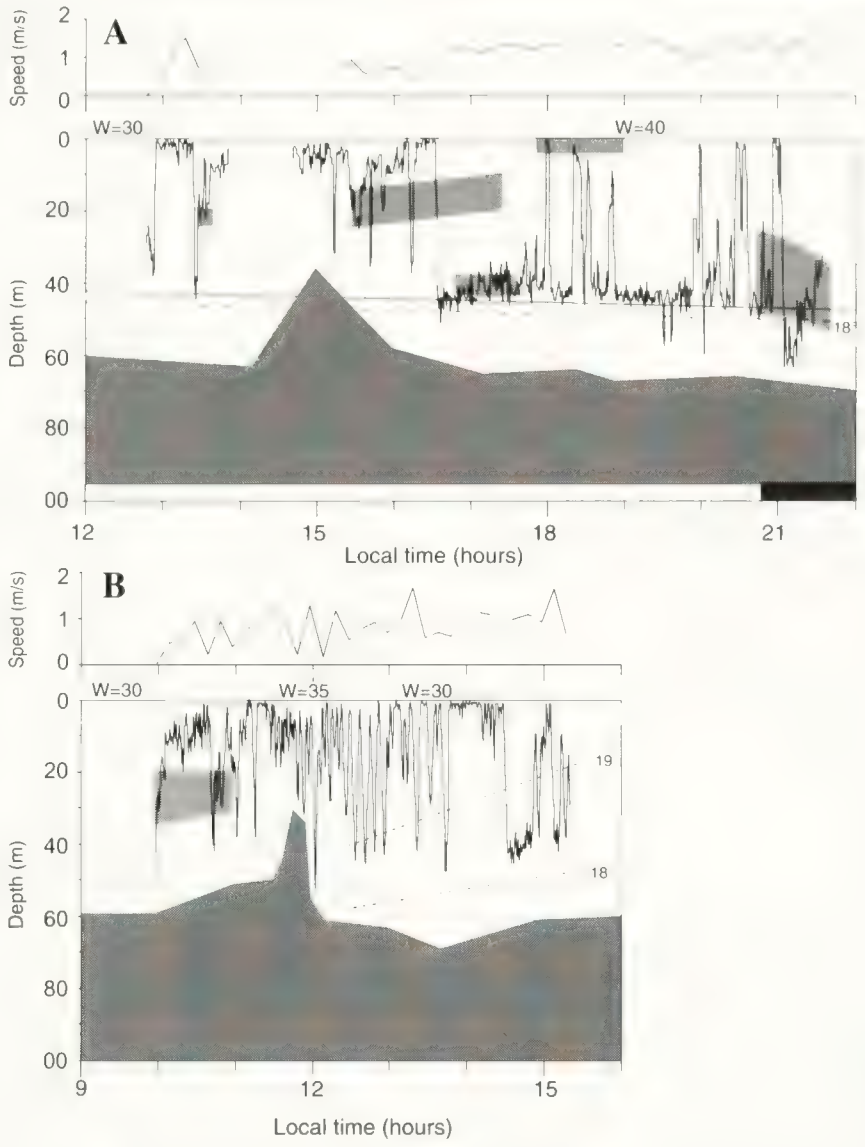

Figure 9

(**A**) Track of southern bluefin tuna 14 on 31 January 1994. (**B**) Track of southern bluefin tuna 16 on 1 February 1994. See Figure 6 for legend details.

proportion of their time (nearly 30%) in the upper 5 m. At night they tend to remain somewhat deeper, although they are present at the surface for part of the night. Tunas 4 and 12 were not surface-oriented during the day, but ranged evenly within the mixed layer. Both these fish were associated with large schools throughout the track and they exhibited rapid vertical oscillations, which we assumed spanned the vertical boundaries of the school. Tuna 6 also spent little time at the surface. It was associated with a small school of tuna and spent most of its time at or below the thermocline while travelling at 2.5 m/s towards the shelf edge. Tuna 14 also spent much of its time at the thermocline boundary while traveling during the day.

Swimming speed

The average swimming speeds of SBT over the entire tracks were in the range of 0.5–1.4 m/s or 0.5–1.4 body lengths/s. These speeds are based on the movements of the tracking vessel and therefore are considered conservative because they do not incorporate the horizontal or vertical meandering of the tracked fish or water currents. There were small differences in the mean speeds between day (0.90 m/s) and night (0.94 m/s) for all fish combined. The frequency distribution of these speeds differed markedly between day and night (Fig. 11). However, the number of observations during the day (n=1119) far exceeded those

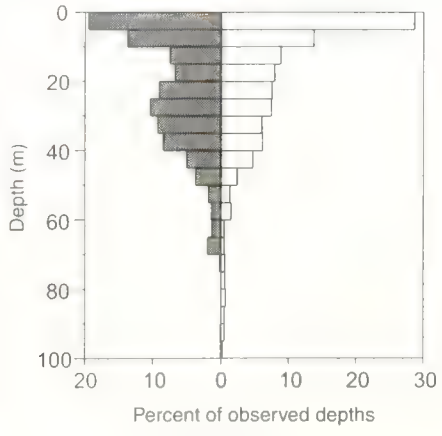

Figure 10

Distribution of observed depths (5-m intervals) by day (open bars) and night (shaded bars) for all tracked southern bluefin tuna.

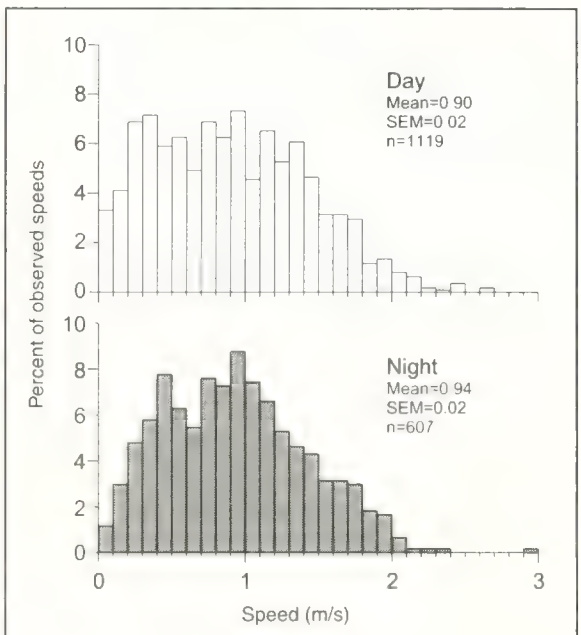

Figure 11

Distribution of observed speeds over the ground (0.1 m/s intervals) by day and night for all tracked southern bluefin tuna.

at night (n=607) and probably accounts for much of the difference in distributions.

Discussion

Horizontal movements

The average swimming speeds of SBT over entire tracks of 0.5–1.4 body lengths/s were similar to the range of mean speeds (0.6–1.0 body lengths/s) for Atlantic bluefin tuna (Lutcavage et al., 2000) and 1.02–1.34 body lengths/s for Pacific bluefin tuna (Marcinek et al., 2001). This is within the range of minimum speeds (0.5–2.0 body lengths/s) required to maintain hydrostatic equilibrium in scombrids (Magnuson and Weininger, 1978). A much higher sustained swimming speed of 2.5 m/s was recorded for tuna 6, which traveled at this speed for 18 hours, virtually in a straight line, from Rocky Island to the shelf break. The vertical movements of this fish were minimized by it orienting itself with the thermocline interface or the surface. And horizontal movements were not apparent. A speed of 2.5 m/s or 2.6 body lengths/s is probably a realistic sustained swimming speed for SBT. Although tunas are obviously capable of high bursts of speed, sustained swimming speeds seem to be very much lower. Yellowfin tuna have been tracked at speeds of 1.2–3.5 body lengths/s, and bigeye tuna at 1.4 body lengths/s (Holland et al., 1990a, Block et al., 1997). The sustained swimming speeds of Atlantic bluefin tuna, determined from sequential aerial photographs, were 0.8–1.6 body lengths/s (NOAA[6]). Brill (1996) considered that the specialized anatomy, physiology, and biochemistry of tuna evolved, not for high burst and sustained swimming speeds as proposed by Dickson (1995), but for rapid growth, digestion, and recovery from exhausting activity.

The horizontal movements and distribution of SBT suggest strong associations with regions of topographical variation or higher temperatures (or both). The SBT were in the warmer waters of the NW region of the study area in 1994, and the tracked fish also remained within areas of warmer water. In 1992 and 1993, all the tuna that traveled some distance swam to waters of similar or higher temperatures. Lutcavage et al. (2000) found that tracked North Atlantic bluefin tuna also traveled on the warm side of surface fronts and that offshore movements were generally associated with offshore warming of deep basins.

The temperatures measured during tracking sometimes did not match up with satellite sea-surface temperatures, owing to the inability of sea surface temperature (SST) algorithms to correct for the variability in atmospheric water vapour, cloud, and aerosols, etc. However, the relative temperature differences considered here appear to be robust. Within these temperature limitations, the tuna were initially located on lumps or near islands. Migration to new areas was often interrupted by brief stays at lumps on the way. The shelf break was clearly the destination of tuna 6. It was tracked near Rocky Island for three hours, before it left abruptly and moved in a straight line to

[6] NOAA (National Oceanic and Atmospheric Administration). 1975. A study of the applications of remote sensing techniques for detection and enumeration of giant bluefin tuna. Southeast Fish. Cent. contrib. no. 437 (MARMAP no. 108), 48 p. National Space Technology Laboratories, Bay Saint Louis, Mississippi 39520.

the shelf break, which it reached some 18 hours later. It remained in that area until tracking ended. These lump, reef, island and shelf-break associations matched the distribution of sightings by aerial survey (Cowling et al.[7]).

Surfacing behavior

Most SBT spend a large part of the day in the upper 10 m (Fig. 10) in the Bight in summer unless they travel to other areas. At night, they tend to move to deeper water, but some tracked tuna remained in the upper 10 m throughout most of the night. The relatively long time spent at the surface during the day in the Bight (nearly 30%) would facilitate sightings by aerial survey, and surfacing behavior would significantly influence aerial detection.

The surface behavior of southern bluefin tuna in the Bight contrasts with that of most other tunas studied. Yellowfin tuna near Hawaii have an average daytime depth of 71 m during tracks offshore and away from fish aggregating devices (FADs), with modes at 0–10 m and 50–60 m. When near FADs, they have an average daytime depth of 59 m. At night, yellowfin have modes at 0–10, 30–40, and 180–190 m (Holland et al., 1990a). Similar depth distributions for yellowfin tuna were observed in the western Pacific (Yonemori, 1982). In the eastern Pacific Ocean, at the northern extent of their range, yellowfin tuna remained at somewhat shallower depths during the day than in previous studies (Block et al., 1997), presumably because of the shallowness of the mixed layer which limited their depth distribution. In the western Indian Ocean, yellowfin tuna tracked both on and off FADs spent most of the day between 60 and 110 m (Cayré and Chabanne, 1986; Cayré, 1991; Marsac et al.[3]).

Tracked skipjack tuna spent little time at the surface during the day in waters off Hawaii (Yuen, 1970; Dizon et al., 1978), and Tahiti (Cayré and Chabanne, 1986), although they were surface oriented at night. In the western Indian Ocean, two skipjack tuna tracks were found at somewhat shallower depths but the modal depths were still between 10 and 20 meters (Cayré, 1991). Bigeye tuna tracked off Hawaii had a modal depth of 220 m during the day and 80 m at night (Holland et al., 1990a). Atlantic bluefin tuna appear to spend some time near the surface in inshore waters off the New England area (Carey and Lawson, 1973), although the modal depth of 0–15 m during the day (Lutcavage et al., 2000) is somewhat deeper than that for SBT in the Great Australian Bight. This nearsurface orientation of Atlantic bluefin tuna has prompted development of aerial surveys to assess the abundance and distribution of these tuna in these waters (Lutcavage and Kraus, 1997). The extensive surfacing behavior of SBT in the Bight does not appear to occur in the shelf waters of the Indian Ocean off Western Australia. Of the six SBT tracked in the west, only one spent significant time at the surface during the day (Fishery Agency of Japan[4,5]). However, this fish oscillated rapidly between 0 and 40 m rather than remaining near the surface. The different surfacing behavior of these SBT in the west may have been due to their much smaller size (35–48 cm compared to 67–114 cm), and that they were in a migratory mode moving southwards, assisted by the Leeuwin Current (Shingu, 1967; Maxwell and Cresswell, 1981), rather than in summer residency.

The conditions in which SBT come to the surface in the Great Australian Bight are quite varied. These tuna remain within the surface 5 m for extended periods during the day under a range of weather and sea conditions, although surfacing is more pronounced on warm days with little wind. A clear example of this type of movement was evident with tuna 9, which remained below the surface in a school of tuna for the first hour of the track, during which winds were documented at over 35 km/h. After the winds dropped, the tracked tuna surfaced and remained there, apart from occasional dives, for the rest of the track. Surface schools of tuna were observed as far as the eye could see during these calm conditions. In contrast, extensive surfacing can occur in adverse weather, as observed in fish 7 between 07:00 and 09:00 h during rough seas and winds >35 km/h. However, in these conditions, no surface fish could be seen from the vessel. Protocols for aerial surveys of SBT in the Bight restrict surveys to wind speeds of <18 km/h because of a marked decrease in school sightings at higher wind speeds (Cowling et al.[7]). The highest number of sightings per unit of effort occurred when aerial surveys were flown in conditions of low wind speeds and little cloud cover. The ultrasonic telemetry suggests that wind affects detection of schools from the air rather than their surfacing behavior.

One of the objectives of the aerial survey was to reduce uncertainty in aerial survey estimates of surface abundance by incorporating environmental and behavioral data into the aerial survey analyses. Although the results from ultrasonic tracking provided preliminary information on vertical distribution that might affect sighting by aerial survey, the intent of our study was to use the more extensive data that would be obtained from archival tags to model responses in surfacing behavior to environmental conditions through space and time. Aerial survey estimates of abundance could then be adjusted by incorporating the proportion of time that SBT would be visible during aerial surveys based on the environmental conditions that occurred at the time of survey flights.

A distinct surfacing behavior regarded as a characteristic of SBT in the Bight during summer is called "rippling" (Hynd and Robins, 1967). This behavior occurs under very calm, sunny conditions. Tuna laze at the surface for extended periods, often breaking this inactive phase by rolling from side to side. Unfortunately we did not have suitable weather conditions to observe this behavior. However, data from archival tags suggest that these fish derive significant heating benefits through both insolation and the transfer of heat from the warm surface waters (Gunn et al.[2]).

[7] Cowling, A., T. Polacheck, and C. Millar. 1996. Data analysis of the aerial surveys (1991–1996) for juvenile southern bluefin tuna in the Great Australian Bight. 1996 Southern bluefin tuna recruitment monitoring workshop report. Rep. RMWS/96/4, 87 p. CSIRO Marine Laboratories, Castray Esplanade, Hobart, Tasmania, Australia 7000.

Reference depths

Reference depths—the depths to which tuna return after regular excursions above or below them—are not well defined in SBT in the Bight. Bounce dives from the surface occur in tracks 1, 3, and 11, and brief excursions above and below the bottom of the mixed layer could be seen in parts of tracks 4, 6, and 14. None of these showed the movements characteristic of bigeye tuna, which use the 15–16° isotherm as a reference point and make regular excursions to the surface (Holland et al., 1990a). These excursions are thought to be a way of regaining optimum body temperature after foraging in cooler deep water (Holland et al., 1990a; Holland et al., 1992). Bluefin tuna have a more advanced vascular anatomy for physiological thermoregulation than bigeye tuna (Holland et al., 1992); therefore one would expect SBT to display less pronounced behavioral thermoregulation than bigeye tuna under the same thermal regime. Unfortunately, the temperature range of the shallow waters of the Bight was also not large enough to induce such a response.

The interface of the surface mixed layer and the thermocline is a reference point used by many tuna species. Yellowfin tuna often remain within this narrow depth band, especially when travelling in a straight line (Carey and Olsen, 1982; Holland et al., 1990a). Traveling fish have been observed to alternate abruptly between the thermocline interface and the surface, which might assist in straight-line orientation (Holland et al., 1990a). Tracks 6 and 14 provide the clearest examples of use of the thermocline interface during sustained straight-line migration. Tuna 6 remained at a depth of about 20 m while staying in the area. However, once it started swimming toward the shelf break, it maintained a relatively constant depth within or just above the thermocline. While this behavior is apparently a characteristic of yellowfin tuna travelling alone (Carey and Olsen, 1982), our tracks were for SBT travelling in schools. Tunas 7 and 8 remained at the surface during fastest straight-line swimming, suggesting that both depth zones might be used during straight-line swimming. Although it appears that the thermocline interface provides some advantage to sustained straight-line movement, it is not clear whether the advantage is in orientation: possibly this temperature range balances heat build-up from sustained swimming.

In contrast to returning to a reference depth, some tracked fish oscillated rapidly within a depth band. This behavior was observed in parts of tracks 4, 7, 10, and 12. This "frenzied" activity might be ascribed to disturbed behavior caused by the tagging or tracking (or both). However, this behavior might reflect individuals traversing the vertical boundaries of the school (Carey and Olsen, 1982). When this behavior was observed in our study, the tracked fish appeared to be part of a school. However, there were many times when the fish was in a school but rapid vertical oscillations were not apparent. Possibly the schools did not extend over sufficient depth range to make this behavior obvious.

Predawn and postdusk dives

A feature of many of the tracks of SBT was the deep dive made just before dawn as the sky began to lighten, and just after sunset before all light was gone. In these dives, the tuna descended rapidly, stayed a short time at the bottom of the dive, and then usually rose gradually to its original depth. These signature dives were observed in tracks 1, 3, 4, 6, 7, 11, 12, 13, and 14 and possibly occurred in other cases obscured by repeated dives over the twilight period. Archival tag data showed clear signature dives in the Bight and more varied behavior off the shelf (Gunn et al.[2]). They also showed that in the central Indian Ocean, SBT dive at dawn, remain at great depth throughout the day feeding on squid, and return to the surface at night. The dawn dives we tracked might correspond to the first part of this movement, but the shelf waters of the Bight are too shallow to have a significant scattering layer, and therefore usually do not allow for the detection of prey. Perhaps this dive at dawn is a fixed behavior that has evolved to locate the scattering layer when SBT are in waters of sufficient depth.

If tuna rely largely on sight to locate prey, twilight would be the first opportunity (dawn), and last opportunity (dusk), in which to find the scattering layer as it rises during the night and descends during the day. Dawn and dusk dives have been observed in eastern spotted dolphin in the eastern tropical Pacific Ocean (Holland[8]). During the day, these dolphin remained in the shallow mixed layer (10–15 m). However, at late dusk they dived to depths of about 65 m. These were followed by further dives, each one a little shallower than the last, until diving was again largely confined to the mixed layer. Just before dawn the pattern was reversed. A line drawn along the bottom of the dives from dusk to dawn would describe a bell shape. The dolphins' behavior was thought to be in response to the vertical movement of the scattering layer. Dawn and dusk dives have since been noted in Atlantic bluefin tuna tracked in shelf waters off New England (Lutcavage et al., 2000) and are apparent in tracks of Pacific bluefin tuna in the eastern Pacific (Marcinek et al., 2001). Block et al. (1997) reported predawn dives in yellowfin tuna tracked in the California Bight. Their vertical track plots suggested that postdusk dives may also occur. Similar vertical behavior has been apparent in the track of one skipjack (Cayré and Chabanne, 1986) and one yellowfin tuna (Carey and Olsen, 1982). However, the absence of similar dives in other studies suggests that the timing of the dives was coincidental.

Stomach temperature

Muscle and stomach temperatures of Atlantic bluefin tuna were monitored in several tracking experiments (Carey and Lawson, 1973; Carey et al., 1984). Both were shown

[8] Holland, K. N. 1996. Personal commun. University of Hawaii, PO Box 1346, Coconut Island, Kaneohe, Hawaii 96744.

to be well above ambient water temperature. Stomach temperature increased after feeding, which was attributed to the hydrolytic processes of digestion and an increase in metabolic rate. Possibly raised stomach temperature speeds digestion and enables a higher feeding frequency when food is abundant. The capacity to maintain higher stomach temperature is enhanced by thermal isolation through heat exchangers, the gas bladder, and the fatty body wall (Carey et al., 1984). Therefore, stomach temperature would reflect activities associated with feeding and digestion, rather than temperature changes occurring in the body. SBT, while very much smaller than the giant bluefin tuna tracked by Carey, also showed a marked differential between stomach and ambient temperatures. The largest differential of 9°C (track 11) was found in the largest SBT tracked, which may be relevant. Because temperature increased steadily during the track, it was probably due to digestion of a meal. All pole-and-line–caught SBT tracked during these experiments were initially chummed with pilchards and could have eaten pilchards just before tracking. In some instances, tunas regurgitated pilchards while the tag was placed in their stomachs. A caecal temperature differential reaching 10°C has also been observed in a 103-cm SBT after being fed in cage experiments (Gunn et al.[9]). The smaller temperature differential observed in the other two tracked tuna (tuna 10 and 13) may have been a consequence of their having less food in their stomach to digest, or their smaller size.

Tuna 11 showed the characteristic changes in stomach temperature associated with the swallowing of prey or water or both. Two swallowing events occurred, a minute apart, resulting in a drop in stomach temperature to ambient temperature. Stomach temperature recovered rapidly, but not quite to the level before swallowing. Carey et al. (1984) managed to have Atlantic bluefin tuna retain tags in their stomachs for up to 13 days by feeding them to ensure that their stomachs never remained empty. Several hours before regurgitation of the tag, a series of cold pulses were observed in stomach temperature, presumably from swallowing water which lowered the stomach temperature briefly. If these cold pulses persisted, the tag would be spat out a few hours later. If the tuna was fed, the tag was usually retained. If regurgitation to purge indigestible items from the stomach normally occurs after digestion is complete and the stomach is relatively empty, as suggested by Carey et al. (1984), then it is likely that the swallowing events observed in tuna 11 involved little or no food. Because a very marked drop in stomach temperature was observed in tuna 11, a large amount of water must have been swallowed.

[9] Gunn, J., T. Polacheck, T. Davis, M. Sherlock, and A. Betlehem. 1994. The development and use of archival tags for studying the migration, behaviour and physiology of southern bluefin tuna, with an assessment of the potential for transfer of the technology to groundfish research. Proc. ICES mini-symposium on migration, St. Johns, Newfoundland. ICES C.M. Mini:2.1, 23 p. International Council for the Exploration of the Sea, Palægade 2-4, DK-1261 Copenhagen K, Denmark.

The effects of chumming on tuna behavior

Observations on tracked tuna being caught up in chumming by commercial pole-and-line fishing have provided us with insights into these operations. Tunas 5, 6, 8, and 15 were associated with chum lines for part of their tracks. They all followed the chum line at a depth of about 20 m for 15–30 minutes, and some came to the surface for brief periods. The tuna schools extended to at least 200 m behind the vessel that was chumming. Pole-and-line operators usually steam forward at about 2 m/s, chumming with live and, sometimes, frozen pilchards. They progress from tuna school to tuna school hoping to combine schools. Most tuna appear to be below the surface and well behind the boat. Fish progress to the front of the school and come to the surface to take chum, replacing tuna that were there before them. Based on our tracking, it appears that tuna after spending a short time at the surface, break away from the chum line in groups or in schools.

Effects of tagging and tracking on tuna behavior

There is a concern that capture, tagging, and tracking procedures change the behavior of the fish being observed. A number of criteria are used to support the view that the fish behave normally: they remain within a school (Yuen, 1970; Cayré, 1991; Cayré and Marsac, 1993); show similarity in vertical and horizontal movements across tracks (Holland et al., 1990a; Cayré, 1991) or through experimental procedures such as evaluating swimming performance when tags are attached externally (Arnold and Holford, 1979; Blaylock, 1990) or observing food consumption when tags are placed in the stomach (Lucas and Johnstone, 1990).

There is however, evidence that SBT do react adversely to being tagged. Hampton (1986) found that lower than expected numbers of SBT tagged with dart tags were recaptured in the first 5 days after release. Also, recaptured fish were in significantly poorer condition than untagged fish—the effect being greatest in those at liberty for 5–20 days (Hampton, 1986) and 13–24 days (Hearn, 1986). Presumably, the adverse effects were related to reduced feeding.

Fish generally undergo a phase of recovery from the trauma of capture and tagging. The resumption of "typical" behavior is often taken as a sign that the fish is behaving normally (Holts and Bedford, 1990). In our study, five tuna initially dived to the bottom, five dived below the depth distribution of the tuna school, and six returned immediately to the school. All returned to schools, which were usually near the surface, within 20 minutes. Most significantly, four tracked tuna actually joined the chum lines of commercial pole-and-line vessels shortly after tagging. However, it could not be determined whether these four tuna were feeding because they did not have temperature-pressure tags in their stomach.

Stress associated with capture and tagging is more obvious in larger fish: blue and striped marlin remain at depth for many hours before returning to normal depths

(Holland et al., 1990b; Holts and Bedford, 1990; Block et al., 1992a). Black marlin dive after release but usually return to normal depths soon after (Pepperell and Davis, 1999). High, sustained, swimming speeds for up to the first six hours of blue marlin tracks were attributed to increased ram ventilation to reduce anaerobic debt (Block et al., 1992b). Undoubtedly there is trauma associated with capture and tagging, but pole-and-line capture is fast, and SBT are not as tired as they would be if caught on a rod and line. In most of the SBT tracks, swimming speed was much slower in the half hour after release than for the remainder of the track. Possibly this slow swimming relates to a recovery phase. However, it more likely reflects the nature of pole-and-line fishing and the association of the chummed school with the boat. After catching and releasing the fish, chumming is stopped. However, the school usually remains with the boat for a short period. The strong schooling behavior of SBT appears to quickly override trauma-induced behavior, such as remaining at depth, that might keep tagged fish away from the school.

Association of the tracked fish with schools is probably the most encouraging sign to the field worker that the tuna is behaving normally, or at least that its movements are representative of the school as a whole. This association was marked in our study. However, on the occasions when the tracked fish appeared to be alone, it was not clear whether this isolation was due to the normal breakup and dispersal of the schools aggregated by the chumming operation or to the tagging and tracking procedure. We were concerned that "herding" (the vessel following the fish influencing the direction of its movements) over a period of time might separate a fish from its school. However, it is also not clear whether it is possible to detect if the tracked fish is solitary or with a school. Depending on the skill and knowledge of the observer, schools can usually be detected in good weather if there is surface or subsurface activity. At night or in rough seas, the usual way of detecting schools is by echo-sounder, but this works only if the school is under the tracking vessel. The school must therefore be large and extend well behind the tracked fish (which is nominally tracked at a distance of 400 m). Often "solitary" tracked tuna displayed the repeated and predictable behaviors seen in other SBT tracks and generally accepted as criteria of "normal" behavior, the most striking of which are the predawn and postdusk dives.

Three methods of tag attachment were used in our study—five tags were attached externally behind the second dorsal fin, ten were placed internally in the stomach, and one tag was accidentally struck by a free-swimming tuna and was attached by the force of the strike. The effects of attaching tags are not currently quantifiable because of the diversity of tuna behaviors. However, the tracks of SBT with stomach tags were more dynamic than the tracks of tuna with tags attached externally. Tunas with stomach tags seemed more responsive to their environment: their behavior included fast, sustained swimming, large translocations, and these tuna were frequently observed with other tuna attracted by chumming operations. Externally attached tags presumably created physical disturbances, such as drag, turbulence, and attachment wounds to which the tuna had to adjust. These are more likely to cause short-term disturbance in behavior than swallowed tags. However, stomach tags had unpredictable, and often short, retention times, which counteracted their advantages.

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Turtle excluder devices—Are the escape openings large enough?*

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Abstract—All five species of sea turtles in continental U.S. waters are protected under the Endangered Species Act of 1973 and the population sizes of all species remain well below historic levels. Shrimp trawling was determined to be the largest source of anthropogenic mortality of many of the species. As a mechanism to reduce the incidental catch of turtles in trawl nets, turtle excluder devices have been required intermittently in the shrimp fishery since 1987, and at all times since 1994. The expanded turtle excluder device (TED) regulations, implemented in 1994, were expected to reduce shrimp trawl capture of sea turtles by 97%. Recent evidence has indicated that the sizes of turtles stranding were not representative of the animals subjected to being captured by the shrimp trawlers. The purpose of our study was to compare the sizes of stranded sea turtles with the size of the TED openings. We compared the sizes of stranded loggerhead (*Caretta caretta*), green (*Chelonia mydas*), and Kemp's ridley (*Lepidochelys kempii*) sea turtles, the three species most commonly found stranded, to the minimum widths and heights of TED openings. We found that annually a large proportion of stranded loggerhead turtles (33–47%) and a small proportion of stranded green turtles (1–7%) are too large to fit through the required minimum-size TED openings. The continued high mortality of sea turtles caused by bottom trawling is reason for concern, especially for the northern subpopulation of loggerhead turtles, which currently is not projected to achieve the federal recovery goal of reaching and maintaining prelisting levels of nesting.

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All five species of sea turtles in continental U.S. waters are protected under the Endangered Species Act of 1973 (ESA, PL93-205). Elasticity models of turtle populations have indicated that the life stages with the highest elasticity are juveniles (i.e. a reduction in mortality in these stages would result in the greatest annual population multiplication rate) (Crouse et al., 1987; Crowder et al., 1994; Heppell, 1998a, 1998b; Epperly et al., 2001; Heppell et al., in press). Size data indicate that the sea turtles most often found dead on ocean beaches are immature (Crouse et al., 1987; STSSN[1]) and shrimp trawling is thought to account for the majority of these deaths (Magnuson et al., 1990; Caillouet et al., 1991, 1996; Crowder et al., 1995). Strandings, however, likely represent only a small proportion of the animals that die offshore (TEWG, 1998).

Beginning in the fall of 1987, the National Marine Fisheries Service (NMFS) seasonally required turtle excluder devices (TEDs) in shrimp trawl nets on most vessels operating in ocean waters off the southeastern U.S. as a mechanism to reduce the incidental catch of turtles in general and the catch of the large immature turtles in particular (Federal Register, 1987); vessels operating off Cape Canaveral and off southwest Florida were required to use TEDs all year. Boats working in inshore waters were allowed to use tow time limits in lieu of TEDs. The difference between offshore and inshore regulations was due, in part, to the lack of information on the distribution and abundance of sea turtles in inshore waters and to the lack of documentation of incidental captures by shrimp trawlers working in these inshore waters (Federal Register 1992a). For the first few years implementation of the regulations was delayed by challenges in the courts and in Congress. The regulations were implemented fully in Spring 1990.

Evidence of the importance of inshore areas to sea turtles, along with evidence that shrimp trawlers catch sea turtles in inshore waters (Epperly et al., 1995; NMFS[2]) provided sufficient justification for NMFS to expand requirements for turtle excluder devices in the shrimp fishery to all areas at all times, including inshore waters; full implementation of these requirements was achieved by December 1994 (Federal Register, 1992a, 1992c). The expanded TED regulations were expected to reduce shrimp trawling capture of sea turtles by 97% (Henwood et al., 1992). Since 1992, TEDs also have been required in the winter trawl fishery for summer flounder operating as far north as Cape Charles, Virginia (Federal Register, 1992b).

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[1] STSSN (Sea Turtle Stranding and Salvage Network). 1998. Unpubl. data. The Sea Turtle Stranding and Salvage Network is a cooperative endeavor between NMFS, other federal agencies, the states, many academic and private entities, and innumerable volunteers. Data are archived at the National Marine Fisheries Service Southeast Fisheries Science Center, 75 Virginia Beach Dr., Miami, FL 33149.

[2] NMFS (National Marine Fisheries Service). 1990. Unpubl. data. NMFS Galveston Laboratory, 4700 Avenue U, Galveston, TX 77551.

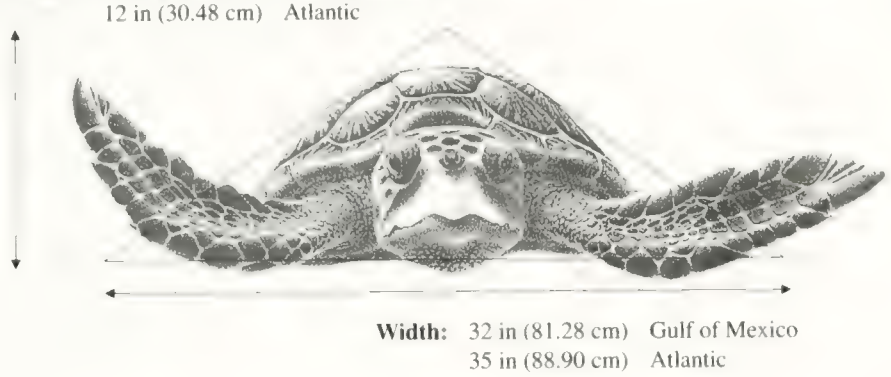

Figure 1

Minimum dimensions (height and width) specified in current U.S. federal regulations (Federal Register, 1992c) for escape openings in single-grid hard turtle excluder devices. The copyrighted figure of the turtle was kindly provided by Jamie Serino of Flying Turtle Productions.

TEDs are equipped with a trap door that allows sea turtles to escape from trawl nets (Seidel and McVea, 1982) and may be either rigid or soft in design (Federal Register, 1992c). To be certified by NMFS, a TED design must be 97% effective, in comparison with a control net, in excluding sea turtles (Federal Register 1987, 1992c). Since 1990, turtles used for TED trials have been small loggerhead turtles, mostly 2-yr-olds that have averaged 34.4 cm SCL (SD=4.1, n=1730, NMFS[3]). Regardless of design, certain parameters of the TED architecture are regulated. Most important to this discussion are the requirements of the height and width dimensions of the opening in the net through which turtles escape. Along the Atlantic Coast these requirements are width ≥35 in (88.90 cm) and height ≥12 in (30.48 cm) (Federal Register,1992c). In the Gulf of Mexico these measurements are ≥32 inch (81.28 cm) and ≥10 inch (25.40 cm), respectively. Height is measured simultaneously with width and is measured at the midpoint of the straight-line distance of width (i.e. the width and height of a taut triangle is measured, Fig. 1).

The purpose of our study was to compare the sizes of stranded sea turtles with the size of the TED openings. This evaluation was prompted by the need, identified by the NMFS Turtle Expert Working Group (TEWG), to reduce the strandings of mature loggerhead sea turtles (*Caretta caretta*) from the northern subpopulation (TEWG, 1998). We compared the sizes of stranded loggerhead, green (*Chelonia mydas*), and Kemp's ridley (*Lepidochelys kempii*) sea turtles, the three species most commonly found stranded, to the minimum widths and heights of TED openings.

[3] NMFS (National Marine Fisheries Service). 2001. Unpubl. data. Galveston Laboratory, National Marine Fisheries Service, 4700 Ave. U, Galveston, TX 77551.

Materials and methods

To compare the sizes of stranded turtles with the minimum size of TED openings we first constructed a predictor of carapace width and body depth. Thus, a morphometric analysis for each species was conducted, generally with data from reared, live captured, or nesting turtles and not with data from strandings. The predictive regression for carapace width was then applied to the strandings data when this measurement was not recorded for a given turtle; the predictive regression for body depth was applied to all turtles in the database because body depth was rarely measured at stranding sites. We then analyzed the entire strandings database to compare turtle sizes with the minimum size of TED openings.

Morphometric analyses

The species-specific relationship between both body depth and carapace width with carapace length was explored through regression analysis and predictive regression equations were developed. Regressions of untransformed data were compared with regressions of $\log_e$-transformed data by comparing goodness-of-fit values.

Morphometric data (straight line carapace length, notch-to-tip [SCL], straight line carapace width [SCW], and body depth [BD]) were recorded by a number of researchers throughout the southeast United States and at the Cayman Turtle Farm, Cayman Islands. Data for loggerhead turtles were concentrated in the 20–30 cm and 30–40 cm SCL size classes and were censored (randomized selection of n=37 in each of the two size classes) to create a more uniform distribution for the analysis (Table 1). Green turtle data were more uniformly distributed across size classes and were not censored (Table 1). Data for Kemp's ridley turtles were concentrated in the 1–10 cm and 10–20 cm

Table 1

Distribution of sizes of sea turtles used in the morphometric analysis.

Straight carapace length (cm)	Loggerhead		Green	Kemp's ridley	
	Frequency	Censored frequency	Frequency	Frequency	Censored frequency
1.01–10	1	1	17	3032	105
10.01–20	1	1	5	3778	105
20.01–30	123	37	37	155	155
30.01–40	629	37	49	58	58
40.01–50	24	24	22	137	137
50.01–60	48	48	21	71	71
60.01–70	26	26	16		
70.01–80	10	10	1		
80.01–90	32	32	3		
90.01–100	27	27	2		
100.01–120	7	7	3		

SCL size classes and were censored (randomized selection of n=105) in each of the two size classes (Table 1).

Strandings analyses

The Sea Turtle Stranding and Salvage Network (STSSN) documents dead or injured sea turtles along the coasts of the eastern United States and the U.S. Caribbean (Schroeder, 1989). The STSSN relies on a trained group of volunteers, including state and federal employees and private individuals, to collect basic biological data on each stranded turtle. Each animal is identified to species, the condition or state of decomposition is determined, standard carapace measurements are taken, and any obvious wounds, injuries, or abnormalities are noted and described. Volunteers who have received additional training may also perform necropsies, or internal exams, on a carcass to determine the general state of health of the animal prior to death, to determine sex, and to locate any obvious internal abnormalities. Data are recorded on standardized report forms that are submitted first to a state coordinator and then to the national STSSN coordinator at the National Marine Fisheries Service, Southeast Fisheries Science Center, Miami, Florida.

The species-specific predictive regression equations from the morphometric analyses were used to estimate the carapace width for each turtle in the STSSN database for which this measurement had not been taken and to estimate the body depth for each turtle. For turtles with curved measurements only, straight line carapace lengths were estimated from curved carapace lengths (CCL) before estimating body depth and carapace width by applying equations reported by Teas (1993).

Within each region (Fig. 2) carapace widths were compared with the currently required minimum widths of TED openings and body depths were compared with the currently required minimum heights of TED openings. Stranded turtles that were reared in captivity, cold-stunned, or known to have been captured incidentally were censored.

Results

Morphometric analyses

Loggerhead sea turtles The relationships between carapace width and carapace length and between body depth and carapace length were linear. Coefficient of determination (r^2) values of regressions with $\log_e$-transformed data were slightly (<0.002) higher than values based on untransformed data. Regression of each of the morphometric values on carapace length was highly significant (P<0.0001) and resulted in the following predictive equations:

$$\ln SCW = -0.0225 + (0.9507 \times \ln SCL) \quad [n=250, r^2=0.989],$$

$$\ln BD = -0.5682 + (0.9100 \times \ln SCL) \quad [n=250, r^2=0.966].$$

Straight line carapace lengths corresponding to turtles with carapace widths of 81.28 cm (32 inch; the minimum width of TED openings in the Gulf of Mexico) and 88.90 cm (35 inch; the minimum width of TED openings in the Atlantic) were 104.5 cm and 114.9 cm, respectively. Straight line carapace lengths corresponding to turtles with body depths of 25.40 cm (10 inch is the minimum height of TED openings in the Gulf of Mexico) and 30.48 cm (12 inch is the minimum height of TED openings in the Atlantic) were 65.3 cm and 79.8 cm, respectively.

Green sea turtles The relationships between carapace width and carapace length and between body depth and

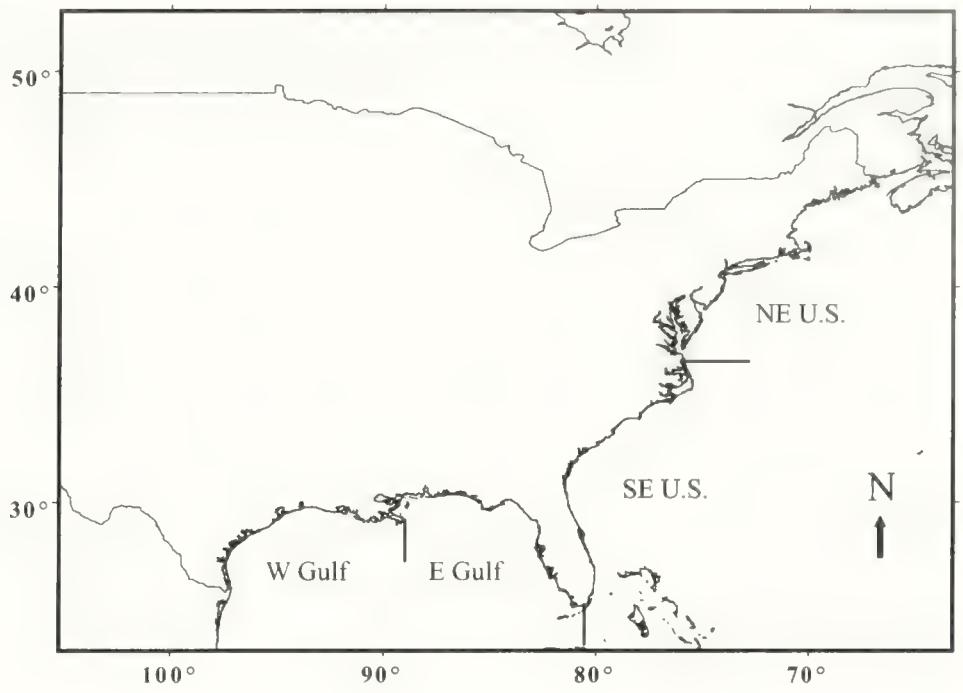

Figure 2

Regions of reported sea turtle strandings along the coasts of the eastern United States and the Gulf of Mexico.

carapace length were linear. Coefficient of determination (r^2) values of regressions with $\log_e$-transformed data were slightly (<0.015) higher than values based on untransformed data. Regression of each of the morphometrics on carapace length was highly significant ($P<0.0001$) and resulted in the following predictive equations:

$$\ln SCW = -0.1608 + (0.9812 \times \ln SCL), \quad [n=176, r^2=0.995],$$

$$\ln BD = -1.0115 + (1.0023 \times \ln SCL), \quad [n=176, r^2=0.977].$$

Straight line carapace lengths corresponding to turtles with carapace widths of 81.28 cm (32 inch) and 88.90 cm (35 inch) were 104.2 cm and 114.1 cm, respectively. Straight line carapace lengths corresponding to turtles with body depths of 25.40 cm (10 inch) and 30.48 cm (12 inch) were 69.2 cm and 83.0 cm, respectively.

Kemp's ridley sea turtles The relationships between carapace width and carapace length and between body depth and carapace length were linear. Coefficient of determination (r^2) values of regressions with $\log_e$-transformed data were slightly (<0.006) higher than values based on untransformed data. Regression of each of the morphometrics on carapace length was highly significant ($P<0.0001$) and resulted in the following predictive equations:

$$\ln SCW = -0.2039 + (1.0437 \times \ln SCL) \quad [n=631, r^2=0.998],$$

$$\ln BD = -0.6283 + (0.9075 \times \ln SCL), \quad [n=631, r^2=0.989].$$

Straight line carapace lengths corresponding to turtles with carapace widths of 81.28 cm (32 inch) and 88.90 cm (35 inch) were 82.2 cm and 89.6 cm, respectively. Straight line carapace lengths corresponding to turtles with body depths of 25.40 cm (10 inch) and 30.48 cm (12 inch) were 70.6 cm and 86.3 cm, respectively.

Strandings analyses

Straight carapace length and width were not measured for a number of stranded sea turtles; body depth almost never was recorded. The total number of records, by species, for which the predictive regressions were applied to estimate straight carapace length or straight carapace width are given in Table 2. Note that the length of a turtle, straight line or curved, must have been measured for the turtle to be included in the analyses because the predictive measures were based on length. It should also be noted that the conclusions from the strandings analyses were not altered by the choice of linear or log-transformed data in the morphometric analyses above.

Loggerhead sea turtles

Carapace width Strandings of loggerhead turtles with carapace widths greater than the currently required minimum widths of TED openings have not exceeded 1%

of the total measured strandings in any year since 1986 (Table 3). The majority of the stranded large (wide) turtles occur in the eastern Gulf of Mexico and the southeast U.S. Atlantic regions, areas where significant nesting occurs.

Body depth Strandings of loggerhead turtles with body depths greater than the currently required minimum heights of TED openings have ranged between 33% and 47% of the total stranded turtles measured every year since 1986 (Table 4]). From 1995 to 1997 nearly 1300 stranded loggerhead turtles were deeper bodied that the currently required minimum TED height opening. The highest proportion of turtles that were too deep bodied to pass through TEDs was found to be in the Gulf of Mexico where TED openings are smaller. The greatest numbers of large turtle strandings occurred on nesting beaches of the eastern Gulf of Mexico and the southeast U.S. Atlantic.

Table 2

The total number of records, by species, for which the predictive regressions were applied to estimate straight line carapace length or straight line carapace width for loggerhead, green, and Kemp's ridley sea turtles.

Missing measurement	Loggerhead	Green	Kemp's ridley
Straight line carapace length	8340	1034	1209
Straight line carapace width	8555	1089	1261

Green sea turtles

Carapace width Strandings of green turtles with carapace widths greater than the currently required minimum width of TED openings have not exceeded two turtles or 2% of the total stranded turtles measured in any year since 1986 (Table 5).

Body depth Strandings of green turtles with body depths greater than the currently required minimum height of TED openings have ranged between 1% and 7% of the total stranded turtles measured since 1986 (Table 6). The large turtles were found sranded in the eastern Gulf of Mexico and the southeast U.S. Atlantic regions, the latter an area of nesting activity.

Kemp's ridley sea turtles

None of the nearly 3000 measured Kemp's ridley turtles that stranded during 1986–97 (total stranded=3476) had carapace widths or body depths greater than the currently required minimum widths and heights of TED openings.

Discussion

All ESA-listed species of sea turtles remain below their historic levels of abundance. The status of Kemp's ridley and loggerhead sea turtles was recently evaluated by the NMFS Turtle Expert Working Group (1998; 2000). Kemp's ridley turtles constitute a single management unit and the nesting population is increasing. If the population continues to grow exponentially, the recovery goal of downlisting

Table 3

Number of stranded loggerhead sea turtles and percentage of those measured with (predicted) carapace widths greater than the minimum width of openings currently required in turtle excluder devices.

	Region of stranding											
	Western Gulf		Eastern Gulf		SE U.S. Atlantic		NE U.S. Atlantic		All regions		Total number measured	Total number stranded
Year	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%		
1986	0	0	2	2	5	1	1	5	8	1	959	1209
1987	1	1	3	2	5	1	0	0	9	1	1318	1728
1988	0	0	5	3	1	0	1	1	8	1	1105	1373
1989	0	0	3	1	1	4	0	0	7	1	1088	1425
1990	0	0	3	3	4	0	0	0	7	1	1258	1592
1991	0	0	2	2	1	0	0	0	3	0	777	975
1992	1	2	0	0	1	0	0	0	2	0	798	1101
1993	0	0	1	1	0	0	1	1	2	0	693	972
1994	0	0	5	7	2	0	0	0	7	1	1044	1342
1995	0	0	1	1	0	0	1	1	4	0	973	1424
1996	0	0	1	1	1	0	2	1	4	0	1461	1883
1997	0	0	6	4	0	0	2	1	8	1	1289	1643

the species from endangered to threatened status (10,000 females nesting in a season) will be met early in this century (TEWG, 2000). There are five known subpopulations of loggerhead turtles in the Western North Atlantic (Encalada et al., 1998; Francisco Pearce, 2001; Francisco et al., in press) but the status of only two could be addressed by the TEWG. Nesting levels of the South Florida subpopulation appear to be increasing, meeting one of the recovery goals set for Florida loggerhead sea turtles. The northern subpopulation, which nests from northern

Table 4

Number of stranded loggerhead sea turtles and percentage of those measured with predicted body depths greater than the minimum height of openings currently required in turtle excluder devices.

	Region of stranding										
	Western Gulf		Eastern Gulf		SE U.S. Atlantic		NE U.S. Atlantic		All regions		Total number
Year	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	measured
1986	68	44	72	89	188	27	4	24	332	35	954
1987	75	54	123	96	225	23	11	25	434	33	1309
1988	62	56	134	96	187	25	6	17	389	38	1027
1989	41	44	209	92	179	26	4	19	433	42	1042
1990	48	36	91	88	250	27	6	22	395	33	1188
1991	37	54	73	83	162	31	18	30	290	40	734
1992	35	58	66	85	198	34	13	28	312	41	763
1993	26	47	76	89	182	40	12	28	296	47	636
1994	97	57	64	88	237	35	15	15	413	41	1010
1995	56	52	66	90	207	30	18	19	347	36	956
1996	99	52	127	88	253	27	33	20	512	36	1436
1997	97	66	131	87	171	23	29	14	428	34	1266

Table 5

Number of stranded green sea turtles and percentage of those measured with (predicted) carapace widths greater than the minimum width of openings currently required in turtle excluder devices.

	Region of stranding											
	Western Gulf		Eastern Gulf		SE U.S. Atlantic		NE U.S. Atlantic		All regions		Total number	Total number
Year	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	measured	stranded
1986	0	0	2	22	0	0	0	0	2	2	101	125
1987	0	0	0	0	0	0	0	0	0	0	122	142
1988	0	0	0	0	0	0	0	0	0	0	178	193
1989	0	0	0	0	0	0	0	0	0	0	223	255
1990	0	0	0	0	0	0	0	0	0	0	280	308
1991	0	0	0	0	0	0	0	0	0	0	200	221
1992	0	0	1	4	0	0	0	0	1	1	184	208
1993	0	0	0	0	0	0	0	0	0	0	180	200
1994	0	0	0	0	0	0	0	0	0	0	268	320
1995	0	0	0	0	0	0	0	0	0	0	312	389
1996	0	0	0	0	1	0	0	0	1	0	508	584
1997	0	0	0	0	0	0	0	0	0	0	286	352

Table 6

Number of stranded green turtles and percentage of those measured with predicted body depths greater than the minimum height of openings currently required in turtle excluder devices.

	Region of stranding										
	Western Gulf		Eastern Gulf		SE U.S. Atlantic		NE U.S. Atlantic		All regions		Total number measured
Year	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	
1986	1	17	3	33	3	4	0	0	7	7	100
1987	2	13	3	12	3	4	0	0	8	7	122
1988	1	11	2	8	2	1	0	0	5	3	177
1989	3	21	3	9	6	3	0	0	12	5	219
1990	0	0	1	2	9	4	0	0	10	4	277
1991	0	0	3	8	3	2	0	0	6	3	196
1992	0	0	2	8	8	6	0	0	10	6	180
1993	0	0	4	11	4	3	1	33	9	5	175
1994	1	2	4	12	9	5	0	0	14	5	258
1995	0	0	1	2	3	1	0	0	4	1	301
1996	1	2	10	9	10	3	0	0	21	4	500
1997	1	3	4	10	7	3	0	0	12	4	282

Florida through North Carolina may now be stable but is currently well below goals set for its recovery (return to prelisting nesting levels). Mortality on at least the northern subpopulation of loggerhead sea turtles needs to be reduced throughout its range to ensure recovery.

Although subpopulations of loggerhead turtles can be easily distinguished by the geographic location of their nesting beaches, the subpopulations comingle on the foraging grounds (Sears, 1994; Norrgard, 1995; Sears et al., 1995; Rankin-Baransky et al., 2001; Witzell et al., 2002; Bass et al., in press). Genetic studies of foraging and stranded animals indicate that the immature benthic animals of the northern subpopulation are distributed along the Atlantic seaboard (Sears, 1994; Norrgard, 1995; Sears et al., 1995; Rankin-Baransky et al., 2001; Witzell et al., 2002; Bass et al., in press), in Florida Bay (Bass et al.[4]), and in the Gulf of Mexico (Bass et al.[5]). Non-nesting adult females from the northern subpopulation appear to occur exclusively along the east coast of the United States with rare exception, and none have been reported from international waters (Bell and Richardson, 1978; Williams and Frick, 2001; CMTTP[6]).

Eight nesting subpopulations were identified for green turtles in the Atlantic Ocean (Encalada et al., 1996), but later were reduced to five regional population units (Bass and Witzell, 2000). Like loggerheads, the subpopulations comingle on the foraging grounds (Bass et al., 1998; Lahanas et al., 1998; Bass and Witzell, 2000). The status of all these subpopulations has not been evaluated, but it appears that nesting levels are increasing on the east coast of Florida (Meylan et al., 1995; Florida Fish and Wildlife Conservation Commission[7]) as well as at Tortuguero, Costa Rica, the largest Western Atlantic rookery (Bjorndal et al., 1999).

A large proportion of stranded loggerhead turtles and a small proportion of stranded green turtles are too large to pass through the required minimum-sizes for TED openings. This finding is corroborated by analyses that suggest that the size distribution of stranded loggerheads is different (larger) than the size distribution of turtles in the nearshore waters (TEWG, 2000). The relatively large proportion of stranded loggerhead turtles with dimensions greater than the minimum height required for TED openings is cause for concern in light of the need to reduce mortality on the northern subpopulation of loggerhead sea

[4] Bass, A. L., M. Clinton, and B. W. Bowen. 1998. Loggerhead turtles (*Caretta caretta*) in Florida Bay: an assessment of origin based on genetic markers. Unpubl. report to Florida Department of Environmental Protection, 5 p. Department of Fisheries and Aquatic Sciences, University of Florida, Gainesville, 7922 NW 71st St., Gainesville, FL 32653.

[5] Bass, A. L., S.-M. Chow, and B. W. Bowen. 1999. Final report for project titled: genetic identities of loggerhead turtles stranded in the Southeast United States. Unpubl. report to National Marine Fisheries Service, order number 40AANF 809090, 11 p. Department of Fisheries and Aquatic Sciences, University of Florida, 7922 NW 71st St., Gainesville, FL 32653.

[6] CMTTP (Cooperative Marine Turtle Tagging Program). 2001. Unpubl. data. The Cooperative Marine Turtle Tagging Program was established by NMFS in 1980 to centralize the tagging programs among sea turtle researchers, distribute tags, manage tagging data, and facilitate exchange of tag information. Since 1999 the CMTTP has been managed by the Archie Carr Center for Sea Turtle Research at the University of Florida, PO Box 118525, Gainesville, FL 32511.

[7] Florida Fish and Wildlife Conservation Commission. 2001. Unpubl. data. 100 Eighth Avenue S.E., St. Petersburg, FL 33701

turtles (TEWG, 1998; 2000) and indicates that, for loggerhead sea turtles, TEDs have not achieved a 97% reduction in captures by shrimp trawlers. Loggerhead turtles are exceeding in size the required minimum height of openings in TED before reaching maturity, especially in the Gulf of Mexico where the allowed opening is smaller than that in the Atlantic. This anomaly had not been noted previously because, since 1990, turtles used for TED trials have been small (<21 cm in body depth, n=1415; NMFS[3]). Based on stage elasticities, a proportional reduction in mortality in the smallest size classes not fitting through the TED openings (large immature turtles) would result in the greatest increased annual population multiplication rate (Crouse et al., 1987; Heppell, 1998a; Epperly et al., 2001). A reduction in subadult and adult mortality from drowning in trawls would benefit all species and subpopulations of sea turtles (Heppell, 1998b).

To decrease the mortality on large turtles caused by trawling, the opening dimensions of TEDs need to be larger than the current minimum requirements and need to be the same in the Gulf of Mexico and the Atlantic. Possible management options include the following: 1) increase the dimensions to accommodate some desired proportion of adults or the total population and 2) adopt the "leatherback" modification (Federal Register, 1993, 1994, 1995) for all areas and all times, which would allow the exclusion of turtles of all sizes, including leatherbacks which are the largest of the sea turtles. In response to our findings, an advance notice of a proposed rulemaking, to effect a change in TED requirements, was issued by NMFS (Federal Register, 2000). After consideration of public comments, NMFS advertised a proposed rule to change the TED requirements (Federal Register, 2001). NMFS should also consider extending the TED regulations to other bottom trawl fisheries of the Gulf of Mexico and along the Atlantic seaboard, including in the Northeast United States, whenever turtles and bottom trawling activity may co-occur.

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Habitat use by demersal nekton on the continental shelf in the Benguela ecosystem, southern Africa.

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Abstract—Videotapes collected by the research submersible *Jago* in the Benguela ecosystem during spring 1997 were analyzed to determine demersal nekton assemblage composition, fish behavior, and microscale habitat association, and habitat selection. Demersal fish assemblage diversity was generally low, and their composition was a function of substratum type. Individual species showed an often marked association with either rocky or soft substrata (or both), and a strong or weak selection for the associated biota. Soles and dragonets actively selected areas of bioactive soft substrata, to which they are behaviorally and morphologically adapted. False jacopever were associated with crevices in areas of high-relief rocky substrata. Kingklip are piscivorous and were largely confined to holes at the base of rocks and favored areas without a conspicuous epifauna. Juvenile hake and gobies avoided extremely rocky areas and were largely indifferent to the presence of benthic invertebrates—behavior that is consistent with their planktonic diets. These results represent the first direct observations of demersal nekton in the region and are important because they allow better interpretations of the results of trawl studies.

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Fish. Bull. 100:475–490 (2002).

The Benguela ecosystem is characterized by dynamic coastal upwelling (Shannon, 1985). It is among the most productive ecosystems in the world (Cushing, 1971) and supports several commercially valuable pelagic and demersal fisheries. Although we have a fairly good understanding of the role that the physical and biological environment play in influencing pelagic fishes (see references in Payne et al., 1987, 1992), the same cannot be said for the demersal species.

Although phytoplankton biomass and production in the Benguela ecosystem are high (Brown et al., 1991), there is a large mismatch with zooplankton (Hutchings, 1992) that results in significant sedimentation (Hutchings, 1992), and periodic anoxia on the bottom (Bailey and Rogers, 1997). Bottom currents are generally sluggish to the south (Shannon, 1985), and the seafloor is characterized by quartz sands, diatomaceous ooze, and foraminiferal deposits (Bailey and Rogers, 1997). Trawl studies have revealed that demersal fish diversity in the region is low and that assemblages can be subdivided into those inhabiting neritic, shelf, and slope areas (Macpherson and Roel, 1987; Roel, 1987; Macpherson and Gordoa, 1992; Smale et al., 1993). Correlations between demersal assemblages and the biophysical milieu (including landscape) have not been made owing to the general lack of environmental data, especially at the microscale.

Submersibles provide a way to sample and observe the biophysical environment of the sea floor. Although the method precludes an appreciation of the infauna, the technique allows for the simultaneous collection of information on the macroscopic benthic fauna and fishes, as well as on the physical features of the environment, across a wide variety of substrata. Elsewhere in the world, submersibles have been used to describe the physical and biological environment of benthic communities (Sibuet et al., 1988) to determine habitat use by nekton (Parker and Ross, 1986; Felley and Vecchione, 1995) and in data collection for stock assessment (Parker and Ross, 1986; Giguère and Brulotte, 1994).

During 1996, the research submersible *Jago* was used to examine some offshore areas near the mouth of the Orange River. A total of 17 dives were made and the archived videotapes were subjected to semiquantitative biological analysis (Gibbons et al., 2000). The *Jago* was commissioned again (by De Beers Marine [Pty.] Ltd.) in 1997 to collect a larger number of higher quality videotapes from the same area. In this article, we report on microscale habitat association and habitat selection by

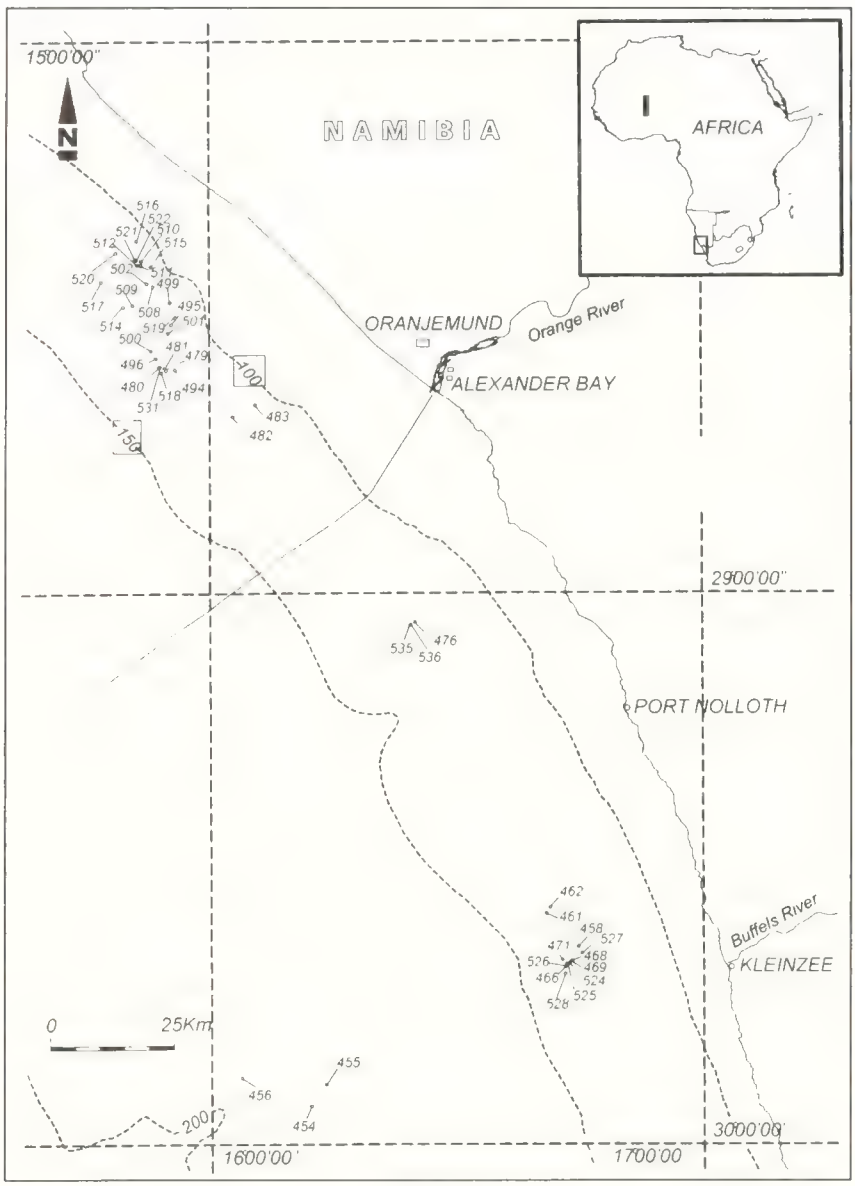

Figure 1

Map of the study area showing location of the dive sites and bathymetry. Numbers represent *Jago* dive numbers.

the common demersal nekton from these videotapes and examine fish behaviors and demersal fish assemblages.

Materials and methods

Field sampling

Videotapes of 44 diving sites in the Orange River delta area between 28°15′S and 29°40′S were analyzed. Surveys were conducted at depths between 100 and 140 m in the middle shelf (Fig. 1). Twenty-six dives were conducted north of the river mouth, and 18 were conducted to the south.

The submersible was launched from a support ship (MV *Zealous*) and towed by an inflatable dinghy to the first way-point of each dive survey. The position of the submersible was tracked every 31 seconds by using an acoustic transponder array. Accuracy of the positioning system was within approximately 5.0 m. A fairly detailed track-chart of the dive was produced and overlaid onto maps of underlying bathymetry.

Videotapes were recorded as the submersible cruised along the seabed (generally at speeds of 0.25 knots) by using a digital video camera. The camera usually faced forward and downward through the front acrylic dome-window and was only occasionally panned or moved during the survey. The submersible stopped at times, either so

Table 1

Distribution of number of samples (n) and area (m^2) in the different areas, among the major substratum types (by nature). Sand = soft sand, of variable texture and topography. With or without biogenic holes. Depth variable. Bioturbation maybe evident. Cobbles = fist-size rocks of claystone, sandstone, or quartzite. Of smooth and rounded appearance. Scattered or aggregated (sometimes densely) on sediment surface, and occasionally projecting through. With or without sediment layer or epifauna. Rock debris = smaller than boulders but larger than cobbles or gravel. Generally of irregular shape and not always smooth. Composed of sandstone or claystone. May project through, or sit on, sediment surface. Scattered or aggregated densely. With or without sediment on upper face. Epifauna maybe present. Boulders = massive, freestanding outcrops of rock, of high vertical relief, generally projecting through the sediment surface. Composed of either sandstone or claystone. Usually with some sediment on upper face. With or without encrusting fauna. Flat bedrock = slab-like sandstone or claystone rock of low vertical relief (<0.5 m), on sediment surface, usually with a thin sediment layer over upper surface. Epifauna on edges.

		North		South	
Major substratum	Substratum nature	n	Area	n	Area
Boulders	hard	3	61.53	1	12.41
Cobbles	hard	12	250.62	0	0
Cobbles	mixed	10	333.71	0	0
Rock debris	hard	40	1008.02	13	239.00
Flat bedrock	hard	9	199.86	0	0
Sand	mixed	97	3158.03	11	316.04
Sand	soft	80	2279.27	105	2123.85

that samples could be collected or to zoom in on particular features, and at other times it moved away from the bottom. Videotape recorded during these times, and when visibility was impaired due to silt disturbance, was not examined. The camera was rarely operated for the full duration of any one dive, and its use depended largely upon the interest of the geological observer. The video camera was equipped with a clock that was synchronized to that aboard the support vessel, so that it was possible to relate sections of the videotape to the actual position of the submersible on the dive-track. Illumination of the sea floor was provided by five 150-W halogen projectors arranged along a bar above the dome-window. A pair of red lasers (positioned 50 cm apart) were projected onto the sea floor to provide a moving scale.

Although the entire videotape from each dive was inspected, only samples of videotape were examined in detail and analyzed. The samples from each tape met the following criteria:

1 they were recorded along linear sections of the dive-track, as determined from the track-chart (to avoid looping and re-examination of previously sampled areas);
2 the submersible was moving at a slow (0.25 knots) but constant speed; and
3 there was no suspended sediment to impair visibility.

Samples were in multiples of selections that were 31 seconds in length. The bottom cover in each sample was first categorized by major (>50%) and subsidiary (>20%) substratum type (see descriptions in legend to Table 1), and then all sedentary biological features were recorded (as present or absent). A total of 381 samples was analyzed, most of which were in the northern area (Table 1). All nekton were identified and counted. Counts were subsequently converted to densities (m^2) with a knowledge of both the horizontal distance traversed by the *Jago* (calculated from the dive track with Autocad [Autodesk Inc., 1988]), and the width of the video-frame (calculated by using the distance between the two lasers, approx. 1–1.5 m).

Statistical analysis

Associations with environmental features The association between nekton and features of the physical and biological environment was examined by following Felley et al. (1989) and Felley and Vecchione (1995). In each sample, the primary substratum was given a score of 0.75, and the subsidiary substratum was allocated a score of 0.25: sedentary biological features were scored as either 1 (present) or 0 (absent). The mean environment was then calculated for each species, after weighting values of each of the environmental variables in each sample by density of individuals in that sample. Samples where no individuals were seen, made no contribution (since they had a weight of 0), whereas samples where the species was abundant made a marked contribution to the species mean. The mean for a variable reflected the relative state of that variable in samples where the species was most likely to be found, and can be thought of as its preference for that variable. A correlation matrix was then generated from all means for the measured environmental variables. Patterns of habitat use by species were reflected in patterns of interrelations among variables. Principal components analysis (PCA) was then performed on the correlation matrix. PCA resolves patterns of interrelationships among variables into a smaller set of composite variables (PCs) to which

observed variables (species abundances) were correlated. Each PC represents a particular trend in habitat use, and the axis differentiates among sets of species that are likely to be found in contrasting conditions for variables that define the PC. Because the PCs define axes, it is possible to plot species on these axes (using the PC scores) and thus identify those with contrasting or similar patterns of habitat use. Species with intermediate scores might be characteristic of intermediate environments, or they might be found over the entire range of environments reflected by a PC (because a species' score is the weighted mean of scores of samples where it was found). Habitat associations by demersal nekton were investigated separately from sites in the north and south because previous observations have suggested that areas to the north and south of the Orange River are distinct (Field et al., 1996).

Habitat selection by individual species can be determined by comparing species' variances on each PC with variance of the environment. Environmental variance on a PC was determined by calculating PC scores for each sample, following standardization with the appropriate mean of means, and standard deviation of means (see Felley and Vecchione, 1995). Then the scoring function was applied to each sample and the variance determined as the variance of sample scores. The score of each sample was assigned to each individual of all species seen in that sample. A species' variance was then calculated for each species as the variance of these scores. Levene's test was used to compare the species' variance with environmental variance. The null hypothesis invoked for these tests was "species" variance is not significantly different from environmental variance with respect to each factor." Active habitat selection by a species was inferred when a species variance was significantly smaller than the observed environmental variance (1-tailed test). This implies that the species was actively selecting a subset of the available environment with respect to that PC, i.e. species distribution in the study area was not random (see Felley et al., 1989). Comparisons of species variances with sample variances on each axis were performed only on the most common species, in each area because the sample sizes for most species were too small to allow statistically meaningful tests.

Assemblages Principal component analysis of the data revealed how species were distributed along composite environmental axes. Although species that are distributed in a similar way on a PC axis can be interpreted to share common responses to that axis, they do not necessarily occur together in the same assemblage. Alternative methods of analysis for examining species associations directly can be used to determine assemblage composition; as an alternative method, the software package PRIMER (Clarke and Warwick, 1994) was used in our study. With this software, descriptive, multivariate statistics allowed an examination of the relationships among the samples (based on similarities in specific composition of nekton) to determine how they were distributed with respect to the physical environment. Abundance of only those species that occurred in greater than 5% of the samples were root-root transformed, and a similarity matrix was constructed between the samples containing two or more species by using the Bray-Curtis index (Field et al., 1982). These matrices were used to plot classification diagrams of percentage similarity between samples by means of group-average sorting (fuller details of this method are provided by Field et al., 1996). Owing to the small area filmed in individual videotape samples (mean 26.20 m^2, SD 11.24 m^2), and the generally low density of most fish species, the samples were pooled (as in Dennis and Bright, 1988) by the nature of the substratum within a dive (hard, soft, mixed), so that replicates were of dives and not of individual videotape samples.

Activities In an effort to understand the behavior of demersal fishes in their natural environment, the activity of each demersal fish (on first sighting) was assigned to one of the following behavior patterns:

1 hovering off the substratum;
2 positioned on the substratum;
3 swimming in the water column;
4 positioned in a crevice or under an overhang;
5 occupying a shelter hole;
6 buried (fully or partially) in the substratum.

Observations of the substratum over which the fish was seen were also recorded, in the hope that it would be possible to correlate behaviors with the environment. The activity of each of the dominant species of demersal fishes was analyzed by using percent occurrence. This value was calculated by dividing the sum of all individuals observed in each activity (per major substratum type) by the total number of individuals of the species for which activities were recorded.

Results

Associations with environmental features

A total of 22 different taxa of demersal nekton were identified from the samples (Table 2). Eight of these were seen only once or twice, and only hakes occurred in more than 50% of the samples. The hakes were assumed to be *Merluccius capensis* on the basis of their inshore distribution (Roel, 1987). It was not always possible to clearly separate gobies, *Sufflogobius bibarbatus,* from dragonets, *Paracallionymus costatus*, and all cases of ambiguity were eliminated (i.e. only those fish that could be identified to species were included in the analyses).

Each species tended to be associated with slightly different features of the physical or biotic environment (or both).

North Eleven species were seen among these samples, and their mean environments are given in Table 3. PCA of the correlation matrix, generated from the mean environments of the six dominant species of nekton, produced three PCs with eigenvalues greater than one (Table 4). PC1 alone explained more than 60% of the variance in the

Table 2

Full list of all demersal nekton observed on the vidoetapes; * = observed once only.

Common name	Scientific name	Common name	Scientific name
Octopus	*Octopus vulgaris*	Kingklip	*Genypterus capensis*
Cuttlefish	*Sepia* spp.	Pelagic goby	*Sufflogobius bibarbatus*
Chokka squid	*Loligo vulgaris reynaudii*	Cape gurnard	*Chelidonichthys capensis*
Sixgill shark	*Hexanchus griseus**	West coast sole	*Austroglossus microlepis*
Smooth hound	*Mustelus mustelus**	Rough scale grenadier	*Caelorinchus simorhynchus*
Izak catshark	*Holohalaelurus regani*	Ladder dragonet	*Paracallionymus costatus*
St Joseph's shark	*Callorhinchus capensis**	Cape dory	*Zeus capensis**
Spearnose skate	*Raja alba**	Monk	*Lophius vomerinus**
Shallow-water Cape hake	*Merluccius capensis*	Cape conger eel	*Conger wilsoni**
False jacopever	*Sebastes capensis*	Snoek	*Thyrsites atun**
Jacopever	*Helicolenus dactylopterus*	Maasbanker	*Trachurus trachurus capensis*

data and contrasted species found over soft bioactive substrata (sole, *Austroglossus microlepis*, and to a lesser extent hakes) with those over more mixed and hard substrata (false jacopever, *Sebastes capensis*). The other species were located midway along this axis (Fig. 2).

PC2 accounted for almost 25% of the variance in the data set (Table 4). The significant loadings on the environmental variables essentially contrasted broken expanses of hard substrata (cobbles, and the biota associated with more open areas) with unbroken expanses of "lifeless" bedrock (Table 4). Those species that were previously contrasted along the PC1 axis were grouped together (false jacopever and sole) and set against those that were positioned midway between them (kingklip, *Genypterus capensis*, and goby) (Fig. 2).

PC3 was responsible for almost 10% of the variance in the data set (Table 4). It can be interpreted in terms of biological richness and contrasted gobies and soles with kingklip and hake (Table 4).

South A total of 10 species were seen in these samples, and their mean environments are given in Table 5. PCA of the correlation matrix generated from the dominant species' means produced four PCs with eigenvalues greater than one (Table 6). The first two PCs explained almost 75% of the variance in the data, although PC1 extracted only ~60%. A clear trend that differentiated the species was determined by PC1, which contrasted dragonets and soles with kingklip and false jacopever (Fig. 2). The loadings on the variables of PC1 (Table 6) opposed hard substrata and their associated epifauna at one extreme with sand and its associated organisms and structures at the other. PC2 contrasted gobies, kingklip, and hake with false jacopever and, to a lesser extent, jacopever, *Helicolenus dactylopterus* (Fig. 2). Interpretation of this PC is difficult because few

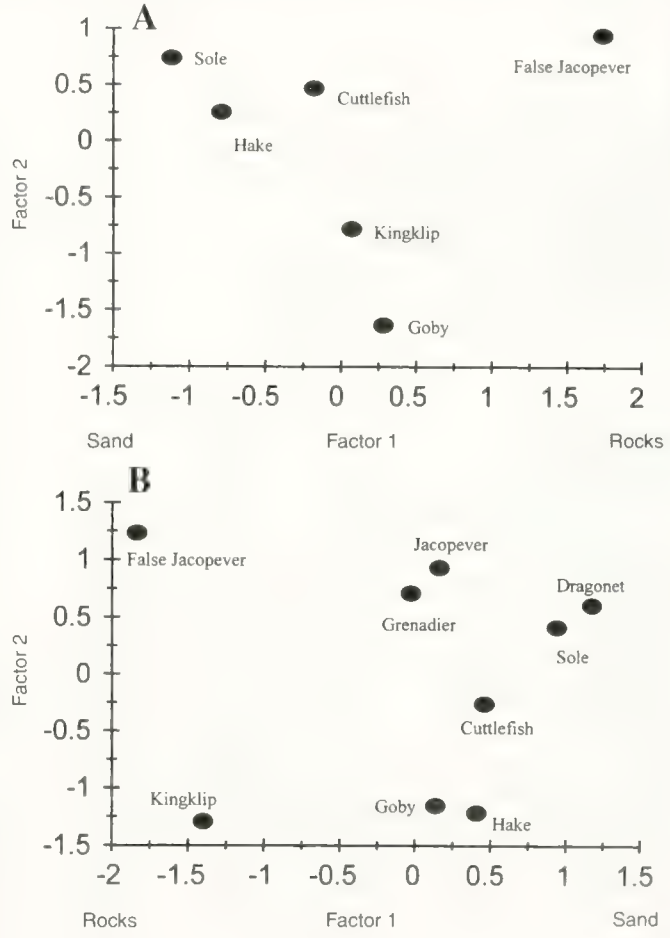

Figure 2

Distribution of species scores along the first and second axes representing habitat use by nekton species in the sites to the north (**A**) and south (**B**) of the Orange River mouth. PC1 (north and south) represented habitat use according to hard and soft substrata. PC2 (north) corresponded to the broken or continuous nature of the substratum, and PC2 (south) represented biological richness (see text).

Table 3

Species means for environmental variables in the undisturbed sites in the northern sampling area. Also given are the sample means total number of individuals of each species seen in samples (n). Data in bold typeface indicate those species used in the principal components

Species	Samples	Area	n	Sand	Cobbles	Debris	Boulders	Bedrock	Mounds
Hake	**177**	**5569.47**	**561**	**0.8266**	**0.0602**	**0.0971**	**0.0058**	**0.0102**	**0.9430**
False jacopever	**34**	**931.3**	**40**	**0.3750**	**0.1188**	**0.3750**	**0.0750**	**0.0563**	**0.7000**
Jacopever	1	18.93	1	0.2500	0	0	0	0.7500	1
Kingklip	**21**	**601.555**	**23**	**0.6087**	**0.0326**	**0.3261**	**0**	**0.0326**	**0.9565**
Goby	**21**	**604.98**	**25**	**0.5000**	**0.0300**	**0.3500**	**0**	**0.1200**	**0.8000**
Gurnard	4	88.2	4	0.8125	0	0.1875	0	0	1
Sole	**11**	**484.99**	**11**	**0.7727**	**0.1591**	**0.0682**	**0**	**0**	**1**
Grenadier	1	18.41	1	0	1	0	0	0	0
Dory	1	20.04	1	0.7500	0	0.2500	0	0	1
Octopus	4	94.86	4	0.6250	0.0625	0.3125	0	0	0.7500
Cuttlefish	**114**	**3721.355**	**183**	**0.7281**	**0.1011**	**0.1380**	**0.0041**	**0.0287**	**0.8852**
Environment	251	7291.03	251	0.6434	0.1116	0.1922	0.0149	0.0378	0.8207

Table 4

Eigenvalues generated from the principal components analysis (PCA) of the species means in the northern study site, using the dominant species only (Table 3). PC loadings of environmental means, and PC scores of the dominant species are also shown. The representations below are of the unrotated principle components. PC loadings greater than 0.50 are in bold typeface. FI, F2, F3 refer to factors 1–3, respectively, generated by the PCA.

	F1	F2	F3
Eigenvalue	9.14	3.481	1.40
% Total variance	60.95	23.21	9.33
Cumulative eigenvalue	9.14	12.62	14.02
Cumulative % variance	60.95	84.15	93.48
Sand	**–0.98**	0.18	0.11
Cobbles	0.34	**0.89**	–0.18
Rock Debris	**0.92**	–0.37	0.02
Boulders	**0.83**	0.49	–0.05
Bedrock	**0.53**	**–0.77**	–0.32
Mounds	**–0.92**	–0.10	0.21
Holes	**–0.83**	–0.47	0.07
Tracks	**–0.55**	–0.33	**–0.71**
Bryozoans	**0.93**	–0.25	0.20
Ascidians	**0.81**	–0.21	–0.51
Sponges	**0.94**	–0.10	–0.14
Cerianthids	**0.54**	**0.62**	0.15
Corals	**0.82**	**0.55**	–0.03
Asteroids	**–0.80**	**0.54**	–0.25
Hake	–0.79	0.26	0.92
False Jacopever	1.73	0.94	–0.20
Kingklip	0.07	–0.78	1.26
Goby	0.28	–1.63	–1.04
Sole	–1.12	0.74	–1.18
Cuttlefish	–0.18	0.47	0.23

of the environmental variables had significant loadings (Table 6); however, it would appear to reflect some level of biological richness.

PC3 accounted for 13% of the variance in the data set (Table 6), whereas PC4 was responsible for only 7%. The significant loadings on the environmental variables of the former contrasted the biota on hard substrata of high relief (boulder and reefs) with the biota of low relief areas (Table 6). PC4 contrasted (much of) the biota with the substrata, although few of the environmental variables had significant loadings (Table 6).

Selection of environmental features

The observed associations between nekton and the biophysical environment were often due to active selection. In the north only hake selected subsets of the available environment based on major substratum type (and its associated biota) (Table 7). This species avoided the rocky extremes, but otherwise showed a pattern of distribution that resembled that of the samples (Fig. 3A). Although false jacopever and hake selected opposite environments based on the broken or unbroken nature of the rock debris (PC2), it would appear that hakes again tended to avoid the extremes (Fig. 3, B and C). The other environmental PCs were not significantly selected for by any species.

Although interpretation of the results generated from the northern data set is confounded by the (mixed) nature of the samples (see Table 1), the same problems did not hamper the data from the south. In the south, six species of demersal nekton selected subsets of the available environment based on the identified axes (Table 7). Hake, goby, sole, and dragonet all appeared to select their environments on the basis of general physical features (PC1). As in the northern area, hake did not show a strong selection for axis extremes (e.g. Fig. 4A), which in itself could mean that hake did not favor very rocky or sandy areas. Dragonets and sole

for each variable, the total number of samples in which each species was seen, and the total area that these represented, as well as the analysis (PCA) (Table 4).

Holes	Tracks	Bryozoans	Ascidians	Sponges	Anemones	Cerianthids	Corals	Asteroids
0.9964	**0.0392**	**0.7023**	**0.3636**	**0.6720**	**0.4920**	**0.0089**	**0.0053**	**0.0784**
0.9000	**0**	**1**	**0.8000**	**0.9000**	**0.5000**	**0.0250**	**0.0500**	**0**
1	0	1	0	1	1	0	0	0
1	**0**	**0.9130**	**0.5652**	**0.7826**	**0.5652**	**0**	**0**	**0**
1	**0.0800**	**0.8800**	**0.7600**	**0.8000**	**0.5600**	**0**	**0**	**0**
1	0	0.7500	0	0.7500	0.7500	0	0	0
1	**0.0909**	**0.7273**	**0.6364**	**0.8182**	**0.2727**	**0**	**0**	**0.0909**
1	0	1	1	1	1	0	0	0
1	0	1	1	1	0	0	0	0
1	0	0.7500	0.5000	0.7500	0.2500	0	0	0
1	**0.0219**	**0.8033**	**0.5574**	**0.7596**	**0.4262**	**0.0219**	**0.0109**	**0.0601**
0.9482	0.0398	0.8048	0.5458	0.7610	0.5219	0.0120	0.0080	0.0478

showed distinct preferences for environments with sandy substrata (Fig. 4, B and C) and were absent from rockier areas. Dragonets and cuttlefish (*Sepia* sp.) appeared to select opposite environments along the PC2 axis, with the former favoring areas with echinoderms and sponges and the latter avoiding them. Hake again appeared to avoid extremes of environment along the PC3 axis, whereas false jacopever selected areas of high relief substrata (Fig. 4, D and E). The results suggest that hake selected areas without cerianthids (and other biota, PC4), whereas dragonet preferred areas with cerianthids (Table 7).

Assemblages

Assemblage composition was a function of substratum type. Cluster analysis of the similarity matrices generated between samples among all the data indicated a similarity in assemblage composition that was generally based on major substratum type (data not shown). These patterns were mirrored in separate analyses of the samples (Fig. 5, A and B). The communities were not always distinct, however, and samples from hard substrata were sometimes grouped with those from mixed, and even soft, substrata. A noteworthy feature of these data was the generally low level of similarity between samples, and this undoubtedly reflected their small individual size (area) and the low density of nekton.

The dendrogram produced by analysis of the species (and not sample) matrix revealed common patterns of association in both the northern and southern areas (Fig. 6, A and B). In the northern area, there were two clusters at the 30% level of similarity (with sole as an out-group) (Fig. 6A). This result is difficult to interpret clearly because the one group comprised species of both soft (hake and cuttlefish) and hard (false jacopever) substrata. These species were also the most abundant and thus the likelihood of their co-occurrence in samples was high. In the south, two groups of associated species were also observed at the 30% level of similarity. The association between hake and cuttlefish was again tight, and both were more distantly linked to false jacopever (Fig. 6B). The other group comprised two clusters at the 40% level of similarity: one of gobies and grenadiers, *Caelorinchus simorhynchus*, and the other of species from soft (dragonets and sole) and mixed substrata.

Activities

None of the dominant species appeared to be either attracted to, or repelled by, the presence of the submersible and its lights, and avoidance behavior was seen only at the moment when the submersible was directly over the fishes.

Few of the fishes seen were actually swimming (behavior pattern 3), and most were resting on the substratum itself (Fig. 7). Indeed, all gobies and soles were seen lying on the substratum. Grenadiers seemed to hover above the substratum, and false jacopever and kingklip appeared to be situated in some sort of shelter. Although a few individual hake, kingklip, and dragonets buried themselves in sand, this behavior was otherwise uncommon. Most of the fish seemed to behave in a similar way over hard and soft substrata. The exceptions to this were kingklip and grenadiers, which tended to hide and rest, respectively, more often over hard substrata rather than soft (Fig. 7).

Discussion

The demersal nekton assemblages over the continental shelf along the west coast of southern Africa are clearly structured in a way that reflects the substratum type. This assemblage composition is in part due to the responses of individual species to the environment. These are novel observations for the region, and they provide a baseline

Table 5

Species means for environmental variables in the undisturbed sites in the southern sampling area. Also given are the sample means total number of individuals of each species seen. Data in bold typeface indicate those used in the PCA (Table 6). T-worms = tube worms.

Species	Fish no.	Samples	Area	Sand	Debris	Boulders	Reefs	Mounds	Holes	Tracks
Hake	**580**	**110**	**2285.12**	**0.987**	**0.013**	**0**	**0**	**0.794**	**1**	**0.331**
False jacopever	**16**	**15**	**347.61**	**0.581**	**0.312**	**0.080**	**0.027**	**0.446**	**0.893**	**0.142**
Jacopever	**7**	**6**	**115.09**	**0.827**	**0.173**	**0**	**0**	**0.821**	**1**	**0.526**
Kingklip	**4**	**4**	**82.73**	**0.564**	**0.436**	**0**	**0**	**0.111**	**1**	**0**
Goby	**14**	**13**	**312.42**	**0.930**	**0.070**	**0**	**0**	**1**	**1**	**0.412**
Gurnard	4	3	67.00	0.901	0.099	0	0	0.250	1	0.250
Sole	**24**	**22**	**414.27**	**1**	**0**	**0**	**0**	**0.967**	**1**	**0.599**
Grenadier	**15**	**14**	**243.65**	**0.668**	**0.332**	**0**	**0**	**0.750**	**1**	**0.661**
Dragonet	**110**	**50**	**853.44**	**1**	**0**	**0**	**0**	**0.988**	**1**	**0.613**
Cuttlefish	**172**	**84**	**1814.90**	**0.935**	**0.061**	**0.004**	**0**	**0.828**	**1**	**0.355**
Environment	130	130	2691.29	0.868	0.118	0.012	0.003	0.717	0.981	0.400

Table 6

Eigenvalues generated from the PCA of the species means in the southern study site, using the dominant species only (Table 5). PC loadings of environmental means, and PC scores of the dominant species are also shown. The representations below are of the unrotated principle components. PC loadings greater than 0.50 are in bold typeface.

	F1	F2	F3	F4		F1	F2	F3	F4
Eigenvalue	10.11	2.56	2.27	1.11	Cerianthids	**0.52**	0.05	0.45	**0.65**
% Total variance	59.45	15.06	13.38	6.54	Corals	**–0.94**	0.24	–0.05	0.03
Cumulative eigenvalue	10.11	12.67	14.94	16.05	Asteroids	**0.72**	0.15	0.43	0.36
Cumulative % variance	59.45	74.50	87.88	94.42	Ophiuroids	0.29	**0.50**	**–0.65**	–0.30
Sand	**0.91**	–0.17	0.30	–0.19	Echinoids	**0.60**	**0.52**	–0.43	0.28
Rock Debris	**–0.85**	0.08	–0.44	0.24	Tube worms	**–0.90**	–0.36	–0.02	0.02
Boulders	**–0.68**	0.46	**0.54**	–0.16	Hake	0.41	–1.21	0.47	–0.63
Reefs	**–0.69**	0.46	**0.52**	–0.17	False jacopever	–1.84	1.23	1.40	–0.46
Mounds	**0.87**	0.17	0.16	–0.34	Jacopever	0.16	0.94	–1.41	–0.77
Holes	**0.69**	–0.46	**–0.52**	0.17	Kingklip	–1.40	–1.29	–0.83	1.24
Tracks	**0.80**	0.45	–0.24	–0.13	Goby	0.14	–1.15	0.27	–1.33
Bryozoans	**–0.99**	0.07	0.01	0.02	Sole	0.94	0.42	0.11	–0.70
Ascidians	**–0.94**	0.08	–0.24	0.21	Grenadier	–0.03	0.72	–1.42	0.30
Sponges	0.07	**0.96**	–0.10	0.20	Dragonet	1.17	0.61	0.84	1.48
Anemones	**–0.98**	–0.06	–0.14	0.00	Cuttlefish	0.46	–0.26	0.58	0.85

set of information that should allow a more meaningful interpretation of the results of the (more typical) trawl surveys for fishes.

Species accounts

False jacopever have been positively correlated with rocky areas from a previous study of the region (Gibbons et al., 2000). Members of the genus *Sebastes* are also known as rockfish and have been reported as common over deep rocky reefs from video-surveys (Richards, 1986; Murie et al., 1994). They seem to prefer structured and high-relief reefs, and a partitioning of the habitat has been observed among congeners (Richards, 1986). Rockfish have been reported as scarce over soft sediments (Stein et al., 1992). Our results are consistent with those from previous studies.

Jacopever was the other scorpionid fish observed in our study. It was far less common than false jacopever and appeared to have a markedly different association with environmental features. Admittedly the sample size for

for each variable, the total number of samples in which each species was seen and the total area that these represented, as well as the

Bryozoans	Ascidians	Sponges	Anemones	Cerianthids	Corals	Asteroids	Ophiuroids	Echinoids	T-worms
0.120	**0.022**	**0.701**	**0.189**	**0.011**	**0.028**	**0.085**	**0.018**	**0.062**	**0.345**
1	**0.668**	**1**	**0.784**	**0**	**0.641**	**0**	**0**	**0**	**0.511**
0.333	**0.333**	**1**	**0.333**	**0**	**0.333**	**0**	**0.209**	**0.138**	**0.155**
0.794	**0.794**	**0.794**	**0.794**	**0**	**0.474**	**0**	**0**	**0**	**0.570**
0.358	**0.094**	**0.745**	**0.390**	**0**	**0.094**	**0**	**0**	**0**	**0.306**
0.645	0.395	0.645	0.250	0	0.395	0	0	0	0.605
0	**0**	**0.979**	**0.030**	**0**	**0**	**0.220**	**0.095**	**0.094**	**0.084**
0.372	**0.333**	**1**	**0.413**	**0**	**0.162**	**0**	**0.080**	**0.203**	**0.331**
0.024	**0**	**1**	**0.024**	**0.053**	**0**	**0.277**	**0.021**	**0.161**	**0.012**
0.203	**0.115**	**0.900**	**0.158**	**0.041**	**0.130**	**0.125**	**0.022**	**0.093**	**0.271**
0.279	0.175	0.825	0.300	0.020	0.141	0.115	0.028	0.065	0.290

Table 7

Distribution tests of individuals of different species on principal components describing environmental use by dominant demersal fishes in the northern and southern study sites. Levene's test of variance equality was used to compare species' variances with variance of samples on each principal component. X and XX indicate a species' variance significantly smaller than location variance at the $P<0.10$ and $P<0.05$ level, respectively (implying that the species uses a subset of available conditions relative to that principal component).

Species	PC1	PC2	PC3	Species	PC1	PC2	PC3	PC4
Hake	XX	XX		Hake	XX		XX	XX
False jacopever		XX		False jacopever			X	
Kingklip				Goby	X			
Goby				Sole	XX			
Sole				Grenadier				
Cuttlefish				Dragonet	XX	XX		X
				Cuttlefish		XX		

jacopever was very small, but it showed a weaker association with high-relief hard substrata and a greater association with more open areas. *Helicolenus dactylopterus* is a conspicuous spcies in trawl catches in the region (Roel, 1987), unlike *S. capensis*, and the difference in habitat use would explain this. Both species are likely to be largely piscivorous as adults (Macpherson and Roel, 1987; Meyer and Smale, 1991), and therefore the association of *S. capensis* with a rich epifauna is more likely an artifact of autocorrelation with hard substrata (per se) than real.

Kingklip have also been correlated with rock cover (Gibbons et al., 2000). Although it is a bycatch species of the commercial trawl fishery over (presumably) mixed grounds (Payne, 1985), a high CPUE is achieved by using long-lines over hard grounds (Badenhorst, 1988). This high CPUE could imply that it is found at greater densities over hard grounds and that the species shows some sort of preference for rocky areas (as suggested by Japp, 1990). In his study of feeding patterns of kingklip, Macpherson (1983) suggested that it probably inhabited holes in the mud (or caves) during the daytime. Our observations indicated that this species hides in holes by day (Fig. 7C), but that these holes are generally at the base of rocks. Such a shelter provides them with ready access to their favored prey (demersal fishes) on the sandy areas surrounding (Macpherson, 1983; Macpherson and Roel, 1987) and would account for a lack of association with conspicuous mobile epifauna..

By contrast, sole have been observed by Stein et al. (1992) to favor areas of soft substrata and tend to be caught in greatest numbers there (Payne, 1985). Both sole and dragonets (Tables 4 and 6) certainly show morphological adaptations to this substratum type and are dorsoventrally flattened to a greater (sole) or lesser (dragonet) extent. These species were also associated with areas having

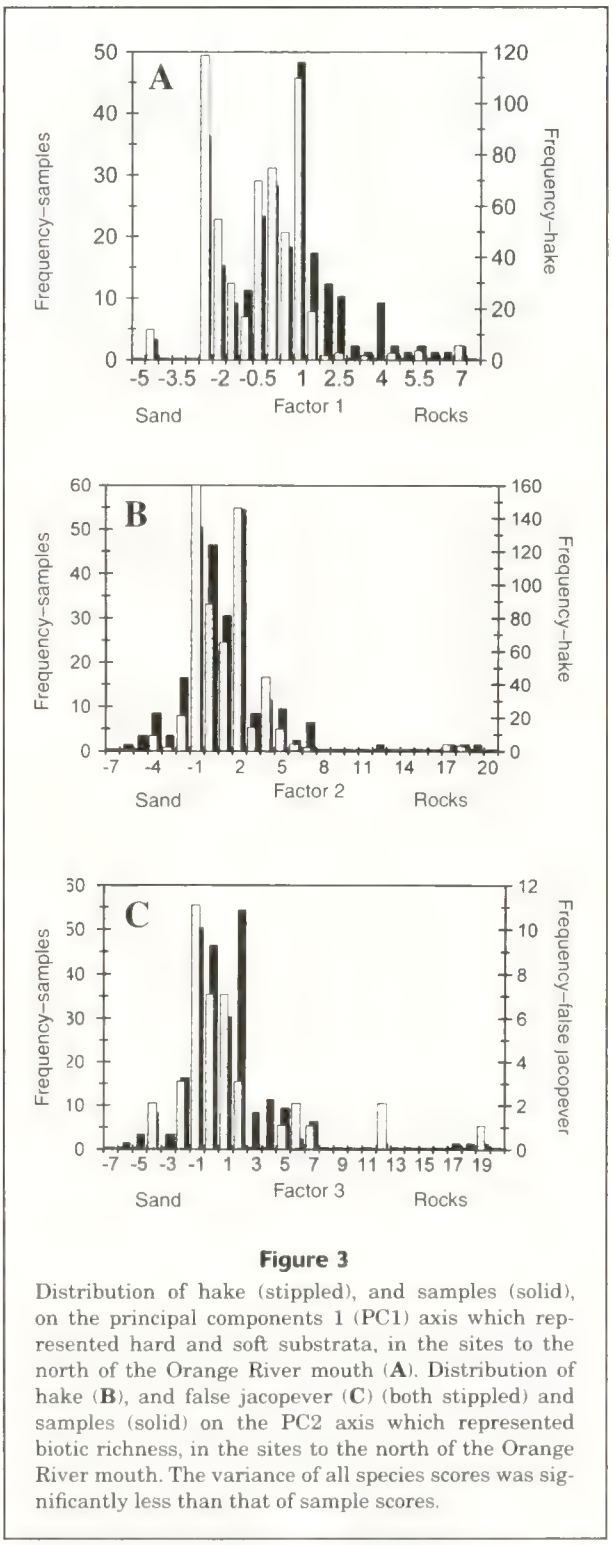

Figure 3

Distribution of hake (stippled), and samples (solid), on the principal components 1 (PC1) axis which represented hard and soft substrata, in the sites to the north of the Orange River mouth (**A**). Distribution of hake (**B**), and false jacopever (**C**) (both stippled) and samples (solid) on the PC2 axis which represented biotic richness, in the sites to the north of the Orange River mouth. The variance of all species scores was significantly less than that of sample scores.

a rich infauna (Table 4), which probably reflects the strictly benthic nature of their diets (Macpherson and Roel, 1987).

An apparent lack of strong habitat preference has been observed by longfin hakes (*Urophycis chesteri*) off North Carolina (Felley and Vecchione, 1995). Although similar results were noted here for *Merluccius capensis* (e.g. Tables 4 and 6), this species tended to avoid the rocky extremes (as in Gibbons et al., 2000). Interestingly, the species was not associated with substrata that were conspicuously rich in either epifauna or infauna. However, because small hake

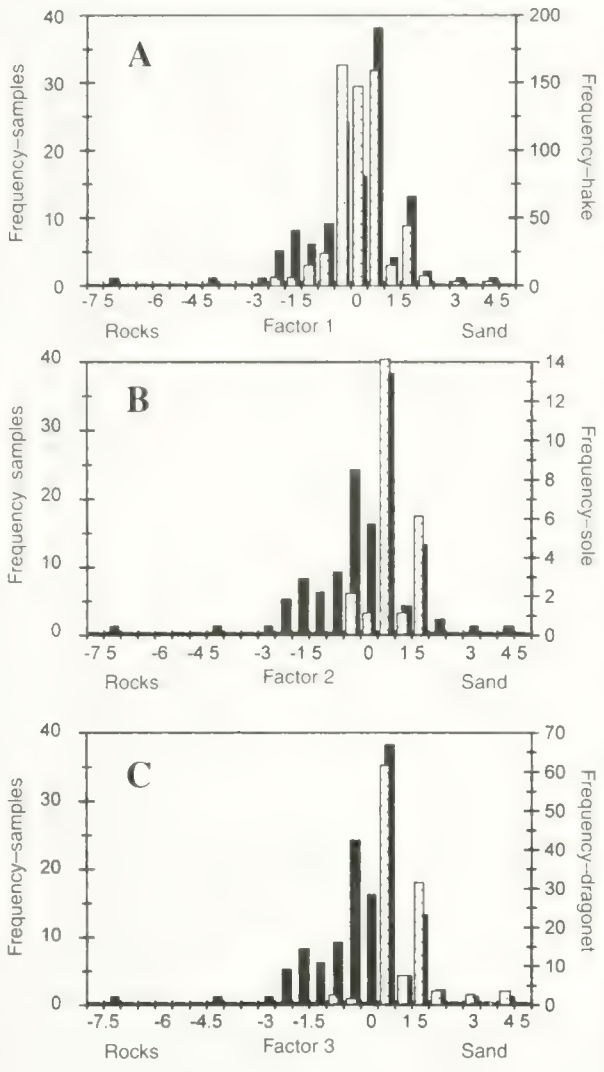

Figure 4

Distribution of hake (**A**), sole (**B**) and dragonet (**C**) (all stippled), and samples (solid) on the PC1 axis which represented hard and soft substrata, in the sites to the south of the Orange River mouth. Distribution of hake (**D**) and false jacopever (**E**)(both stippled), and samples (solid) on the PC3 axis which represented vertical structure, in the sites to the south of the Orange River mouth. The variance of all species scores was significantly less than that of sample scores.

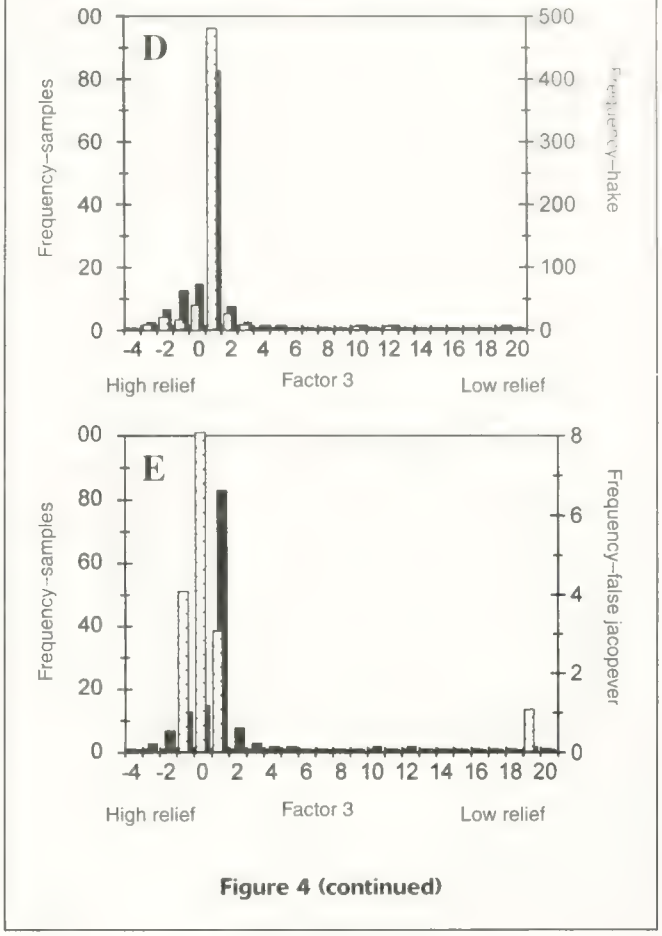

Figure 4 (continued)

display strong vertical migration at night and feed primarily on macrozooplankton (Pillar and Barange, 1995), a pronounced association with a benthic fauna need not be expected. Should the use of the demersal environment by hake during the day, therefore, simply be one of a place to rest, then the preference for sandy areas needs to be interpreted in terms of favored shelter. Our observations of hake behavior (Fig. 7A) indicated that most individuals were positioned immediately on the sand, although some were buried in the upper layers of the substratum. Under the white lights of the *Jago*, these juvenile hake were pink and blotchy in color and appearance and were not strongly different from kingklip, and it is possible that such an appearance may serve to camouflage individuals.

Cuttlefish are well known to use camouflage, and this may account for the fact that they were not strongly associated with soft or hard substrata (Tables 4 and 6). Cuttlefish are the commonest cephalopod caught in demersal trawls (Japp, 1997), implying that they are known to occur over sandy and mixed substrata. Cuttlefish feed predominantly on fishes and crustaceans (Lipinski, 1992) and therefore the lack of any strong association with ophiuroids is to be expected.

Grenadiers, on the other hand, tended to be associated with brittlestars (Table 6). Unlike cuttlefish, however, grenadiers are known to feed quite extensively on ophiuroids[1] and small epifauna (Meyer and Smale, 1991) and did not seem to show any strong association with extremes of substrata and were observed in both soft and hard habitats (Table 5). The smaller species of macruorids (such as *C. simorhynchus*) form a small but conspicuous part of the

[1] Adriaans, W. 2000. Unpubl. data. Zoology Department, University of the Western Cape, Private Bag X17, Bellville 7535, South Africa.

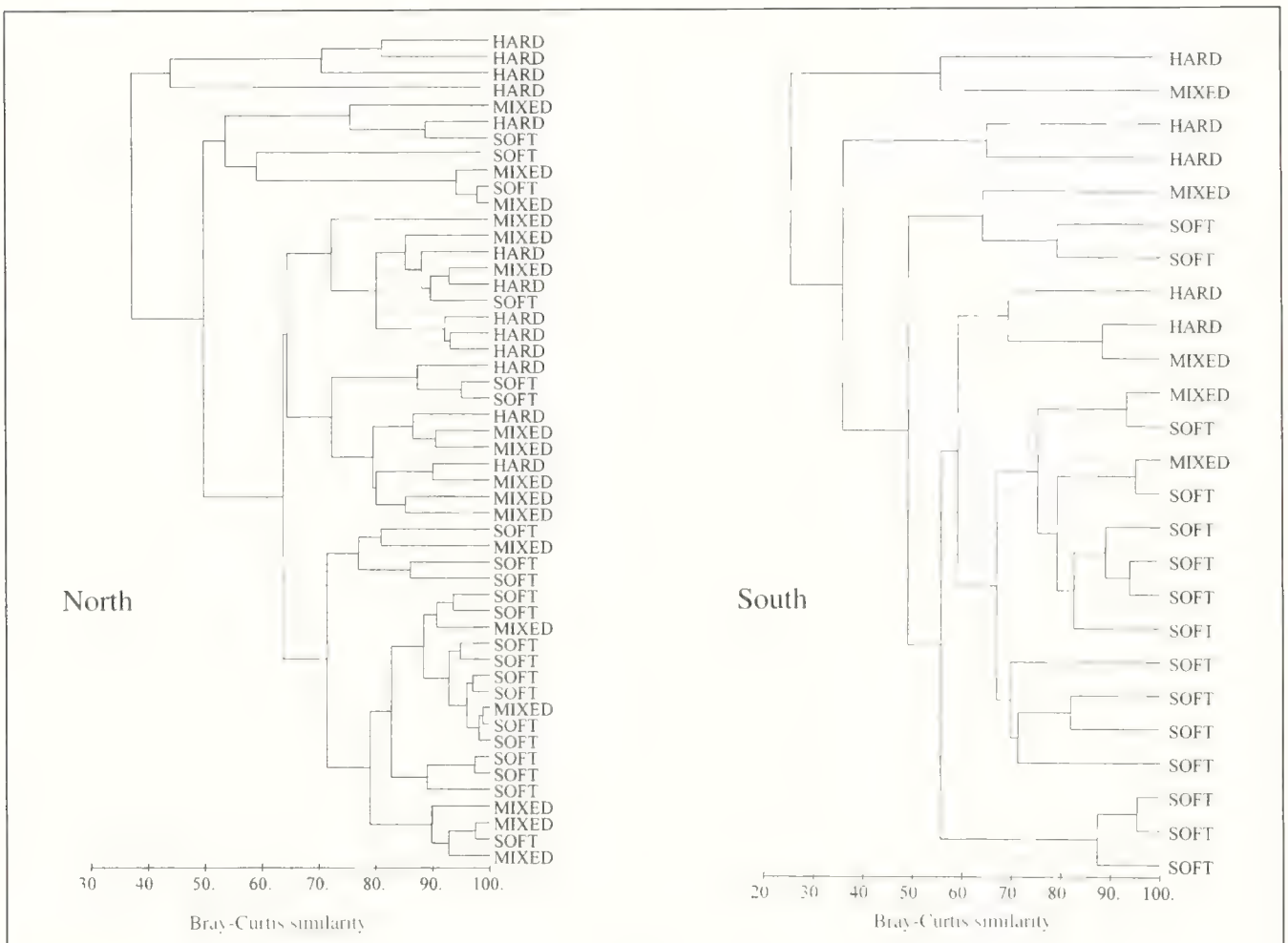

Figure 5

Cluster analysis of the pooled (by major substratum per dive) samples of nekton collected over the areas to the north and south of the Orange River mouth.

bycatch from the hake-directed trawl fishery and are thus assumed to occupy a wide range of habitats.

The gobies seen in our study tended to show neither a strong association with any substratum type (and their associated biota), nor were they linked to areas with a rich ophiuroid fauna (Tables 4 and 6). *Sufflogobius bibarbatus* is also known as the pelagic goby because it spends much of its time at night in the water column,[2] where it forms a conspicuous part of the fish community[3] and where it feeds largely on zooplankton.[2] If the gobies observed in our study were *S. bibarbatus* (as postulated), then the data suggest that their use of the demersal habitat by day was primarily linked to shelter. Otherwide, it might be expected that they would be associated with areas rich in benthic food, such as ophiuroids, which are known to form part of the diet of other gobies (Gibson, 1982).

Communities

The overall diversity of the fish community observed by the *Jago* is less than that determined from the same region with trawl nets (Roel, 1987), principally because the area sampled was significantly smaller. The diversity of the fish and cephalopod fauna may also seem low by comparison with submersible surveys elsewhere (e.g. Felley et al., 1989). But, this region is not known to support a high diversity of demersal species (Mas-Riera et al., 1990) because of the perceived harshness of the prevailing environment (such as frequent intrusions of low-oxygen bottom water (Bailey and Rogers, 1997)).

The demersal nekton fauna, both as individual species and as a whole, was strongly influenced by substratum type (as in Parker et al., 1994). Despite the large research effort

[2] Pillar, S. C. 2000. Personal commun. Marine and Coastal Management, Cape Town, South Africa.

[3] O'Toole, M. 2000. Personal commun. Ministry of Fisheries and Marine Resources, Windhoek, Namibia.

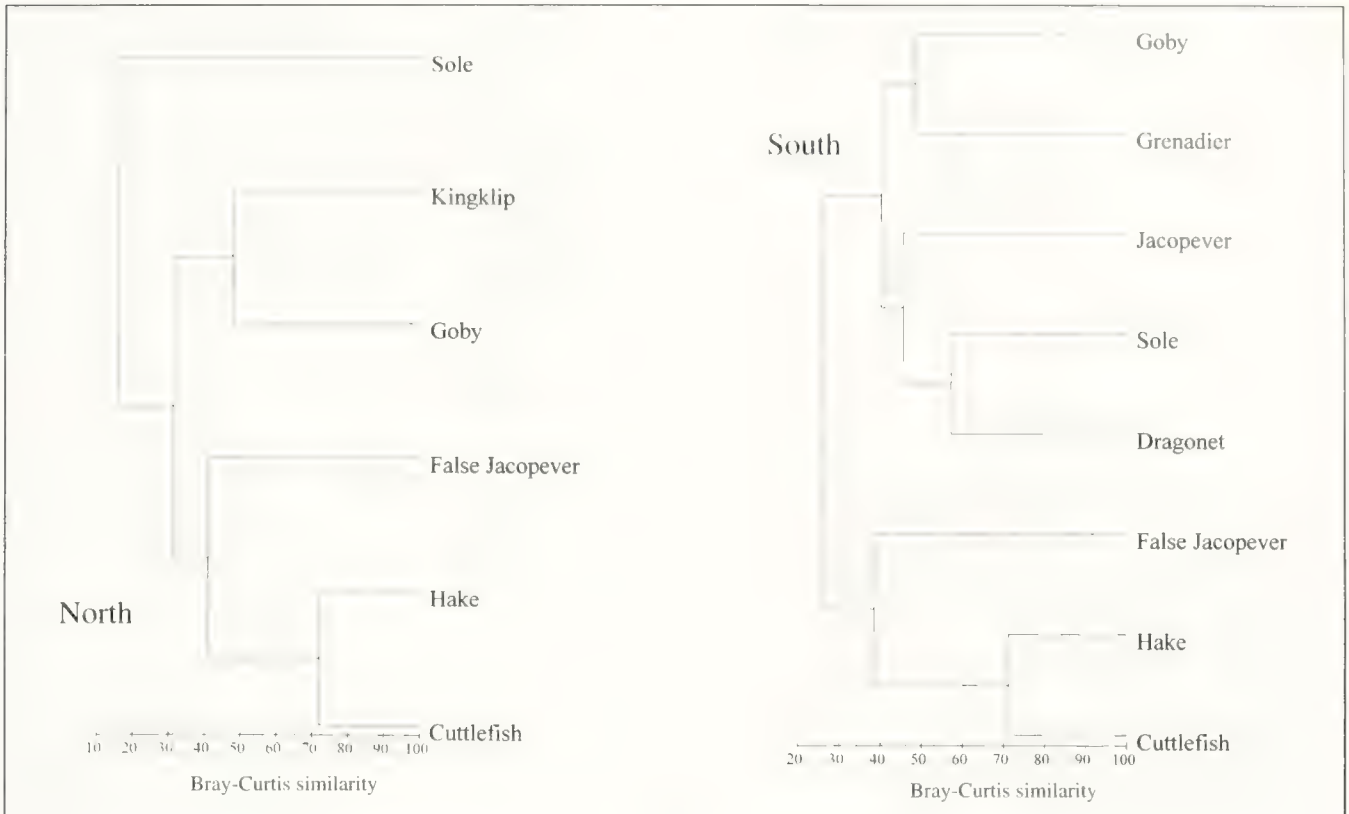

Figure 6

Inverse classification diagram showing species' associations among all the samples (pooled by major substratum and dive) collected in the sites to the north and south of the Orange River mouth.

that has focussed on the commercially important demersal fisheries along the west coast of southern Africa, there is a dearth of published material that can be usefully compared to the current observations. Roel (1987) recognized that the species composition of the demersal fauna in the southern Benguela ecosystem was mainly influenced by depth, and she identified two distinct communities of demersal nekton. One of these was dominated by *Merluccius paradoxus* and occurred at depths greater than 380 m, and the other was dominated by *M. capensis* and was confined to the continental shelf. In the northern Benguela ecosystem, Macpherson and Roel (1987) recognized five distinct demersal fish communities. Two of these were distributed over the shelf (and were subdivided by latitude), and the balance was essentially depth related and ran parallel to the coastline, offshore. Similar observations on the structure of the demersal fish assemblages were made by Macpherson and Gordoa (1992) and Mas-Riera et al. (1990), who noted that latitudinal variations in community composition were generally associated with the state of upwelling. The latter authors postulated that the especially low level of diversity of the demersal fish community in the northern Beguela ecosystem (the region of our study) was due to the presence of low-oxygen bottom water. The "indicator" species for the assemblage in their analysis included *Merluccius capensis* and *Sufflogobius bibarbatus*, which were also among the common species observed in our study.

Smale et al. (1993) observed three demersal communities over the Agulhas Bank (south coast of South Africa) which were related to depth; inshore (<100 m), shelf (90–190 m), and slope (>200 m). Although the species observed in the our surveys were all conspicuous components of the shelf communities identified by the these authors, they were relatively rare (or absent) from the samples collected by Smale et al. (1993). Unfortunately, the nature of these authors' data (30–60 minute trawls) is such that they do not provide any fine-scale information on species associations, and this effectively limits further comparison.

There appears to be a difference in the community of fishes from the northern and southern study sites (e.g. the presence of dragonets in the south but not in the north). Differences in the infaunal communities from undisturbed sites to the north and south of the Orange River were noted by Field et al. (1996). Gibbons and Sulaiman[4]

[4] Gibbons, M. J., and A. Sulaiman. 1998. A video-description of the mid-shelf benthic environment off the west coast of southern Africa, with a comment on the habitat association of demersal nekton. A report to De Beers Marine (Pty) Ltd., Cape Town 8000, Republic of South Africa, 62 p.

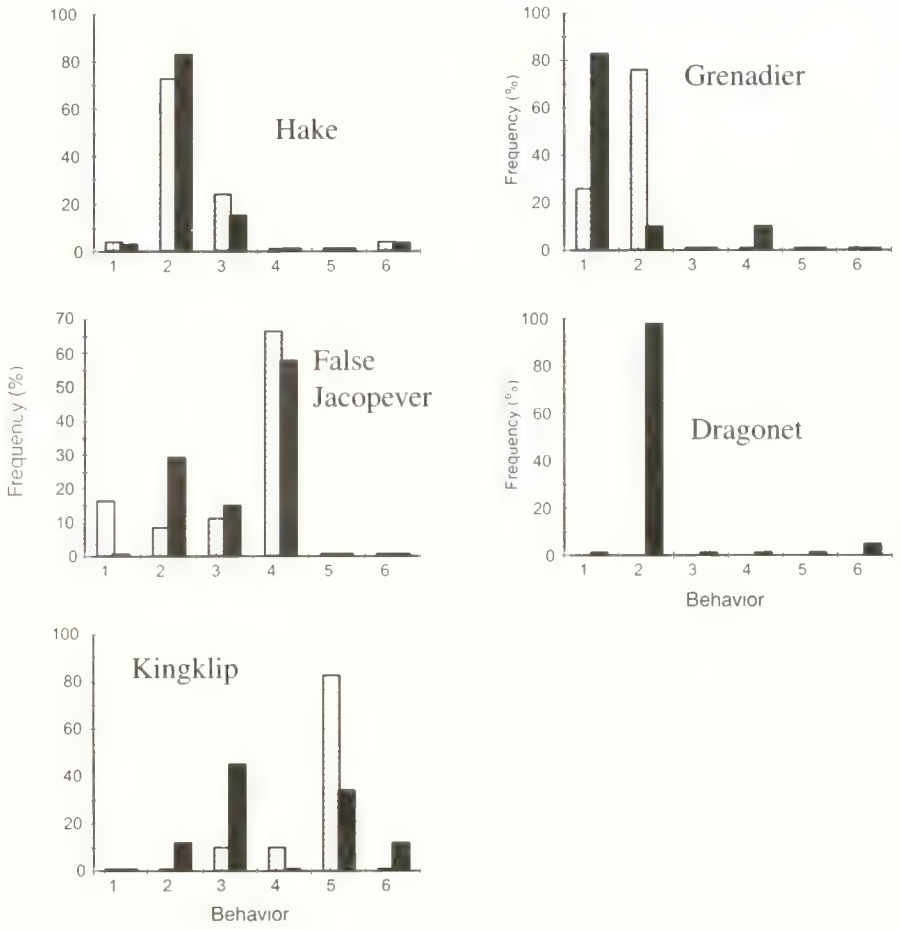

Figure 7

Histograms showing the frequency (as percent) at which behavior patterns 1–6 were observed (x-axis) in species videotaped during survey dives between 100–140 m in the Orange River delta area, southern Africa. All data were pooled. Behavior patterns: 1 = hovering off the substratum; 2 = positioned on the substratum; 3 = swimming in the water column; 4 = positioned in a crevice or under an overhang; 5 = occupying a shelter hole; 6 = buried (fully or partially) in the substratum. Solid bars indicate behaviors over soft substrata, stippled bars indicate behaviors over hard substrata.

also commented on some discrepancies in the structure of the physical and biological environment in regions to the north and south of the Orange River, which can be partly explained by the latitudinal influence of the River and by biogeography (Emanuel et al., 1992; Gibbons and Hutchings, 1996).

Acknowledgments

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Population structure of king mackerel (*Scomberomorus cavalla*) around peninsular Florida, as revealed by microsatellite DNA*

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Abstract—A total of 1006 king mackerel (*Scomberomorus cavalla*) representing 20 discrete samples collected between 1996 and 1998 along the east (Atlantic) and west (Gulf) coasts of Florida and the Florida Keys were assayed for allelic variation at seven nuclear-encoded microsatellites. No significant deviations from Hardy-Weinberg equilibrium expectations were found for six of the microsatellites, and genotypes at all microsatellites were independent. Allele distributions at each microsatellite were independent of sex and age of individuals. Homogeneity tests of spatial distributions of alleles at the microsatellites revealed two weakly divergent "genetic" subpopulations or stocks of king mackerel in Florida waters—one along the Atlantic coast and one along the Gulf coast. Homogeneity tests of allele distributions when samples were pooled along seasonal (temporal) boundaries, consistent with the temporal boundaries used currently for stock assessment and allocation of the king mackerel resource, were nonsignificant. The degree of genetic divergence between the two "genetic" stocks was small: on average, only 0.19% of the total genetic variance across all samples assayed occurred between the two regions. Cluster analysis, assignment tests, and spatial autocorrelation analysis did not generate patterns that were consistent with either geographic or spatial-temporal boundaries. King mackerel sampled from the Florida Keys could not be assigned unequivocally to either "genetic" stock. The genetic data were not consistent with current spatial-temporal boundaries employed in stock assessment and allocation of the king mackerel resource. The genetic differences between king mackerel in the Atlantic versus those in the Gulf most likely stem from reduced gene flow (migration) between the Atlantic and Gulf in relation to gene flow (migration) along the Atlantic and Gulf coasts of peninsular Florida. This difference is consistent with findings for other marine fishes where data indicate that the southern Florida peninsula serves (or has served) as a biogeographic boundary.

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Fish. Bull. 100:491–509 (2002).

The king mackerel (*Scomberomorus cavalla*) is a coastal pelagic fish distributed in the western Atlantic Ocean from Massachusetts (USA) to Rio de Janeiro (Brazil) and in the Gulf of Mexico and Caribbean Sea (Rivas, 1951; Collette and Nauen, 1983). Recreational and commercial catches of king mackerel in U.S. waters are substantial (Manooch, 1979; MSAP[1]; Legault et al.[2]) and the species is critical to the southeastern Atlantic coast (hereafter "Atlantic") and northern Gulf of Mexico (hereafter "Gulf") charter-boat industries. Management of the king mackerel resource in U.S. waters is under the jurisdiction of two regional fishery management councils, and current management planning (GMFMC[3]) is based on a two migratory unit (stock) hypothesis: one stock (Atlantic migratory unit) occurs in the U.S. southeastern Atlantic, the other (Gulf of Mexico migratory unit) occurs in the Gulf. Separation of the two stocks has been based primarily on mark-and-recapture studies carried out prior to 1984 and on differences in growth rate (MSAP[1]; Williams and Godcharles[4]). Based on the mark-and-recapture studies, it was hypothesized that the two stocks mixed extensively during

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[1] MSAP (Mackerel Stock Assessment Panel). 1994. Contribution report of the mackerel stock assessment panel. Contribution report MIA-93/94-42, 27 p. Southeast Fishery Science Center, National Marine Fisheries Service, 75 Virginia Beach Dr., Miami, FL 33149.

[2] Legault, C. M., M. Ortiz, G. Scott, N. Cummings, and P. Phares. 2000. Stock assessment analyses on Gulf of Mexico king mackerel. Contribution report SFD-99/00-83, 48 p. Southeast Fishery Science Center, National Marine Fisheries Service, 75 Virginia Beach Dr., Miami, FL 33149.

[3] GMFMC (Gulf of Mexico Fishery Management Council). 1996. Amendment 8 to the fishery management plan for coastal migratory pelagic resources in the Gulf of Mexico and South Atlantic includes environmental assessment, regulatory impact review, and initial regulatory flexibility analysis. Gulf of Mexico Fishery Management Council, 3018 U.S. Hwy, 301 North, Suite 1000, Tampa, FL 33619-2266.

[4] Williams, R. O., and M. F. Godcharles. 1984. Completion report, king mackerel tagging and stock assessment. Project rep. 2-341-R, plus figures and tables., 45 p. FL Dept. Nat. Res., Florida Marine Research Institute, 100 8th Ave. SE, St. Petersburg, FL 33701.

the winter months along the southeast coast of Florida. For purposes of stock assessment and resource allocation (Sutter et al., 1991; GMFMC[5]), the boundary between the two stocks was specified as the Volusia/Flagler county line (east coast of Florida) in winter (1 November–31 March) and the Monroe/Collier county line (west coast of Florida) in summer (1 April–31 October). Pragmatically, this means that king mackerel caught south of the Volusia/Flagler county line (including the Florida Keys) between 1 November and 31 March belong to Gulf stock, whereas fish caught south of the Monroe/Collier county line between 1 April and 31 October belong to Atlantic stock.

Data from additional mark-capture (Fable et al., 1987; Sutter et al., 1991; Schaefer and Fable, 1994; Fable[6]), growth rate (DeVries and Grimes, 1997), otolith shape (DeVries et al., 2002), and temporal-geographic sampling studies (Collins and Stender, 1987; Trent et al., 1983; Grimes et al., 1990) are consistent with the hypothesis that king mackerel in the Atlantic differ from those in the Gulf. In addition, on the basis of allozyme evidence (Johnson et al., 1993) and studies of early life history (Grimes et al., 1990; Grimes et al.[7]), DeVries and Grimes (1997) suggested that there might be two distinct stocks of king mackerel in the northern Gulf. Johnson et al. (1993) found a high frequency of the *PEPA-2a* allele of the nuclear-encoded dipeptidase (*PEPA-2*) locus among king mackerel from the western and northwestern Gulf, whereas a high frequency of the *PEPA-2b* allele occurred among king mackerel from the Atlantic and northeastern Gulf. Johnson et al. (1993) hypothesized that the two (putative) Gulf stocks mixed to varying degrees in the northern Gulf. Considering all the data acquired to date, DeVries and Grimes (1997) suggested there may be three stocks of king mackerel in U.S. waters: one in the Atlantic, one in the eastern Gulf, and one in the western Gulf.

The allozyme data of Johnson et al. (1993) did not distinguish king mackerel in the eastern Gulf from those in the Atlantic, and to that extent, argued against the hypothesis that king mackerel in the Atlantic and Gulf represented two distinct stocks. Gold et al. (1997), however, assayed variation in restriction sites of mitochondrial (mt)DNA among king mackerel collected from 13 localities along the U.S. Atlantic coast and northern Gulf and found significant (but weak) heterogeneity only in comparisons of pooled mtDNA haplotypes from Atlantic localities with pooled haplotypes from Gulf localities. Thus, the mtDNA data did not support the hypothesis that two genetically identifiable stocks of king mackerel occur in the northern Gulf, but rather were consistent with the hypothesis that separate stocks of king mackerel may exist in the Atlantic and in the Gulf. Estimates of F_{ST}, a measure of population subdivision, between king mackerel in the Atlantic and Gulf were small, indicating that mixing between Atlantic and Gulf king mackerel occurs.

Gold et al. (1997) also examined spatial variation in frequencies of the two alleles at *PEPA-2*. Results were essentially the same as those reported by Johnson et al. (1993): high frequency of the *PEPA-2a* allele among king mackerel in the western Gulf and high frequency of the *PEPA-2b* allele in the eastern Gulf and Atlantic. Tests of independence of *PEPA-2* genotypes with age and sex of individual fish, however, revealed significant nonrandom associations among Gulf fish of *PEPA-2a* homozygous genotypes with males and of *PEPA-2b* homozygous genotypes with females. Moreover, among fish sampled from the Atlantic, there was a highly significant decrease in the frequency of *PEPA-2b* alleles with increasing fish age. The same trend was found among fish sampled from the Gulf, but to a lesser extent. Tests of independence of sex versus age, and of mtDNA variation versus sex or age, were nonsignificant. These findings strongly indicated that the use of *PEPA-2* genotypes to distinguish stocks of king mackerel is compromised and that the hypothesis of eastern and western stocks of king mackerel in the Gulf needs to be re-evaluated.

Finally, Broughton et al. (2002) surveyed allelic variation at five nuclear-encoded microsatellites among a subset of the samples of king mackerel studied by Gold et al. (1997). Tests of homogeneity in allele distribution at the five microsatellites indicated that samples from Port Aransas, Texas (western Gulf), and Gulfport, Mississippi (central Gulf), differed from each other and from the remaining samples (including two samples from the Atlantic, one from the Florida Keys, one from the eastern Gulf, one from the western Gulf, and one from Veracruz, Mexico). No significant differences in allele frequencies at any microsatellite were found between samples representing geographic extremes, and no significant geographic patterns were found when samples were combined into regional groupings reflecting current hypotheses of king mackerel stock structure in U.S. waters.

Of concern to management of the king mackerel resource in U.S. waters is the degree of mixing between the presumed stocks in the Atlantic and Gulf. Analysis of mark-and-recapture data collected from 1985 to 1993 (MSAP[1]) indicated that roughly 3.0% of fish tagged in the Atlantic were recaptured in the Gulf, whereas 6.4% tagged in the Gulf were recovered in the Atlantic. More liberal estimates (SFC[8]) of recaptures (generated when utilizing summer

[5] GMFMC (Gulf of Mexico Fishery Management Council). 1984. Final amendment 1, fishery management plan and environmental impact statement for coastal migratory pelagic resources (mackerels) in the Gulf of Mexico and South Atlantic region. Gulf of Mexico Fishery Management Council, 3018 U.S. Hwy, 301 North, Suite 1000, Tampa, FL 33619-2266.

[6] Fable, W. A., Jr. 1988. Stock identification of king mackerel based on mark-recapture. Unpubl. manuscript from meeting on stock identification of king mackerel in the Gulf of Mexico. Southeast Fish. Sci. Center Contribution Report 2-18-88, 24 p. Southeast Fisheries Science Center, 3500 Delwood Beach Road, Panama City, FL 32408.

[7] Grimes, C. B., J. H. Finucane, and L. A. Collins. 1988. Distribution and occurrence of young king mackerel, *Scomberomorus cavalla*, in the Gulf of Mexico. Unpubl. manuscript from meeting on stock identification of king mackerel in the Gulf of Mexico. Panama City Lab. Contribution Report 2-18-88, 31 p. NMFS SE Fish. Cntr., 3500 Delwood Beach Road Panama City, FL 32408.

[8] SFC (Southeastern Fisheries Center). 1992. Preliminary analysis of southeastern U.S. king mackerel mark-recapture data: 1985–1993. Contribution report MIA-93/94-36, 19 p. Southeast Fisheries Science Center, National Marine Fisheries Service, 75 Virginia Beach Dr., Miami, FL 33149.

and winter seasons in the "mixing" zone) suggested that 2.6–30.9% of recaptured tagged-fish in the Atlantic were returned as Gulf fish and 1.5–13.6% of recaptures tagged in the Gulf were returned as Atlantic fish. These mixing rates, however, were questioned (Jones et al.[9]) because virtual population analysis (VPA) based estimates of fishing mortality for the directed king mackerel fisheries in the Gulf and Atlantic corresponded to annual exploitation rates of 0.30 and 0.11, respectively, whereas exploitation rates calculated from the 1985–93 (uncorrected) tag returns ranged from 0.027 to 0.033 (Gulf) and from 0.036 to 0.045 (Atlantic). The difference between the two estimates of exploitation rates implied either that the true exploitation rate was overestimated by VPA or underestimated by uncorrected tag-return data, leading to the conclusion (Jones et al.[9]) that little confidence should be placed in reported mixing rates based on mark-and-recapture data.

The goals of this project were to use nuclear-encoded microsatellites to define more rigorously the spatial-temporal limits of the two stocks (if separate stocks exist) and to estimate the proportions of both stocks in the mixing zone. The issues of spatial-temporal limits and mixing of the two (presumed) stocks are important in relation to assessing and allocating the king mackerel resource, particularly during the winter season. For example, mark-recapture data (MSAP[1]) indicated that ~20% of fish tagged in the mixing zone in southeastern Florida moved into the Gulf. If this means that only ~20% of winter catches from the east coast of Florida are Gulf stock, as opposed to 100% under the current management plan, the allowable biological catch (ABC) for the Gulf stock would decrease significantly (MSAP[1]). Because the Gulf stock of king mackerel currently is considered overfished (Legault et al.[2]) reductions in ABC of the Gulf stock could have significant economic impact.

The choice to employ microsatellites for the project was straightforward. Briefly, microsatellites are rapidly evolving, short stretches of DNA composed of di-, tri-, and tetranucleotide arrays that are abundant, highly polymorphic, and inherited in a codominant fashion (Weber, 1990; Wright, 1993; Wright and Bentzen, 1994). Because allele frequencies at microsatellites are generally consistent with equilibrium expectations of diploid, Mendelian loci and because identification of individual microsatellites is by polymerase-chain-reaction (PCR) amplification, both of which remove most of the problems associated with homology of alleles, microsatellites have proven to be useful genetic markers of population structure in numerous taxa, including fishes (Angers and Bernatchez, 1998; Ruzzante et al., 1996; O'Connell et al., 1998; Nielsen et al., 1999). In addition, new alleles at microsatellite loci appear to arise rapidly (Schug et al., 1998), generating high allelic diversity important for statistical power in exact tests and other tests of allele-distribution homogeneity (Estoup et al., 1998; Ross et al., 1999).

Materials and methods

A total of 20 samples of king mackerel were procured between 1996 and 1998 from 11 different offshore sites (Table 1, Fig. 1). The sample from Panama City was obtained from charter boat catches, and the samples from Sarasota and Jacksonville were obtained from tournaments. The remaining samples were obtained from commercial catches. Tissue samples (heart and muscle) were removed from each fish, frozen in liquid nitrogen, transported to College Station, and stored at –80°C. Sex of individuals was recorded for all samples, except for the March 1997 sample from the Florida Keys. Approximate ages of individuals from all samples except for the July 1998 sample from Jacksonville, the March 1997 sample from the Florida Keys, and the April 1997 sample from Sarasota, were determined by otolith-increment analysis by following methods outlined in DeVries and Grimes (1997).

Initially, we planned to deploy the five microsatellites developed in a prior study (Broughton et al., 2002). Two of these (*Sca-8* and *Sca-47*), however, had proven difficult to amplify consistently in the prior study and therefore were omitted from our study. A third microsatellite, *Sca-30*, developed by Broughton et al. (2002), also was omitted because of difficulties with consistent amplification and because allele distributions at *Sca-30* were highly leptokurtic (Broughton et al., 2002). A total of five new microsatellites was then developed from the microsatellite-enriched genomic library generated by Broughton et al. (2002). Candidate microsatellites were sequenced from either or both ends by using standard M13 sequencing primers and an Applied Biosystems (Perkin Elmer) 377 automated DNA sequencer. The OLIGO software package (National Biosciences, Inc., 1992) was used to identify primers from regions flanking microsatellites. Primers were designed according to preset criteria that included product length, internal stability, proportion GC content, and primer Tm difference. PCR amplifications were performed under a variety of experimental conditions to optimize procedures that produced high yields of target sequence and minimized additional fragments ("stutter" bands). Experimental tractability (reproducibility, consistency, range in allele size, frequency of "stutter" bands [if present], and microsatellite polymorphism) of PCR-amplified microsatellites were evaluated by screening a panel of king mackerel samples available in the laboratory. PCR primer sequences, the length (in base pairs) of the cloned allele, and the annealing temperature in PCR amplification for the seven microsatellites used in the project are given in Appendix Table 1. Two of these, *Sca-37* and *Sca-44*, were developed previously by Broughton et al. (2002).

For assay of individual fish, genomic DNA was isolated from frozen tissues as described in Gold and Richardson (1991). Genotypes at the seven microsatellites were determined by PCR amplification and gel electrophoresis. Prior

[9] Jones, C. M., M. E. Chittenden, and J. R. Gold. 1994. Report to the mackerel stock identification working group. Unpubl. document of meeting held 8 Sep 94 to 9 Sep 94 at Panama City Lab., SE Fish. Sci. Cent. 7 p. Southeast Fisheries Science Center, National Marine Fisheries Service, 3500 Delwood Beach Road, Panama City, FL 32408.

Table 1

Localities, acronyms, dates of collection, and number of individuals (by sex) of king mackerel (*Scomberomorus cavalla*) sampled from the east and west coasts of Florida and the Florida Keys.

Sample locality	Acronym	Date of capture	Number of individuals			Migratory group[1]
			Female	Male	Total	
Atlantic Ocean (east coast)						
Jacksonville, FL	JCK[1]	Jul 1996	48	0	48	Atlantic
Jacksonville, FL	JCK[2]	Jul 1998	28	3	31	Atlantic
New Smryna Beach, FL	NSB	Jul 1996	41	9	50	Atlantic
Cape Canaveral, FL	CCN	Dec 1998	24	26	50	Gulf
Sebastian, FL	SEB[1]	Mar 1997	29	21	50	Gulf
Sebastian, FL	SEB[2]	Mar 1998	24	26	50	Gulf
Sebastian, FL	SEB[3]	Dec 1998	35	15	50	Gulf
Ft. Pierce, FL	FTP	Apr 1996	31	25	56	Atlantic
West Palm Beach, FL	WPB	May 1998	29	25	54	Atlantic
Florida Keys						
Key West, FL	KEY[1]	Mar 1996	41	10	51	Gulf
Key West, FL	KEY[2]	Mar 1997	—	—	29	Gulf
Key West, FL	KEY[3]	Jan 1999	29	19	48	Gulf
Gulf of Mexico (west coast)						
Marco Island, FL	MCI	Apr 1996	29	26	55	Atlantic
Boca Grande, FL	BCG	Apr 1996	31	4	35	Gulf
Sarasota, FL	SAR[1]	Apr 1996	39	5	44	Gulf
Sarasota, FL	SAR[2]	Nov 1996	60	0	60	Gulf
Sarasota, FL	SAR[3]	Apr 1997	55	2	57	Gulf
Sarasota, FL	SAR[4]	Apr 1998	68	2	70	Gulf
Sarasota, FL	SAR[5]	Nov 1998	62	6	68	Gulf
Panama City, FL	PCY	Oct 1996	25	25	50	Gulf

[1] Classification as Atlantic or Gulf migratory group based on the two migratory unit hypothesis where boundaries change seasonally. See text for further details.

to amplification, one of the primers was kinase-labeled with γ^{32}P-ATP by T4 polynucleotide kinase (30 min, 37°C). PCR reactions contained approximately 5 ng of genomic DNA, 0.1 units of *Taq* DNA polymerase, 0.5 μM of each primer, 800 μM dNTPs, 1–2 mM $MgCl_2$, 1X *Taq* buffer at pH 9.0 (Promega, Corp., Madison, WI), and sterile deionized water in a total volume of 10 μL. Thermal cycling was carried out in 96-well plates as follows: denaturation (45 sec, 95°C), annealing (30 sec, temperature as in Appendix Table 1), and polymerization (30 sec, 72°C) for 30 cycles. Aliquots (3 μL) of each PCR reaction were electrophoresed in 6% denaturing polyacrylamide ("sequencing") gels. Gels were dried and exposed to x-ray film. Alleles at individual microsatellites were scored as number of repeats by comparison to the cloned (and sequenced) allele. Genotypes at each microsatellite for each individual were scored and entered into a database.

Initial statistical analysis involved generation of allele frequencies and (direct-count) heterozygosity values, and significance testing of genotypic proportions in relation to those expected under conditions of Hardy-Weinberg equilibrium. Significance testing of Hardy-Weinberg equilibrium proportions involved exact tests performed using Markov-chain randomization (Guo and Thompson, 1992); probability (P) values for tests at each microsatellite within each sample were estimated by permutation (bootstrapping) with 1000 resamplings (Manly, 1991). Significance levels for simultaneous tests were adjusted with the sequential Bonferroni approach (Rice, 1989). Tests of genotypic equilibrium at pairs of microsatellites were carried out as a surrogate to assess whether any microsatellites were genetically linked. Probability values for (exact) tests of genotypic equilibrium were generated by 1000 resamplings, and significance levels for simultaneous tests were adjusted with the sequential Bonferroni approach. Allele frequencies and heterozygosity values were obtained by using BIOSYS-1.7 (Swofford and Selander, 1981), and tests of Hardy-Weinberg and genotypic equilibrium employed the package GENEPOP (Raymond and Rousset, 1995). Exact tests also were used to test independence

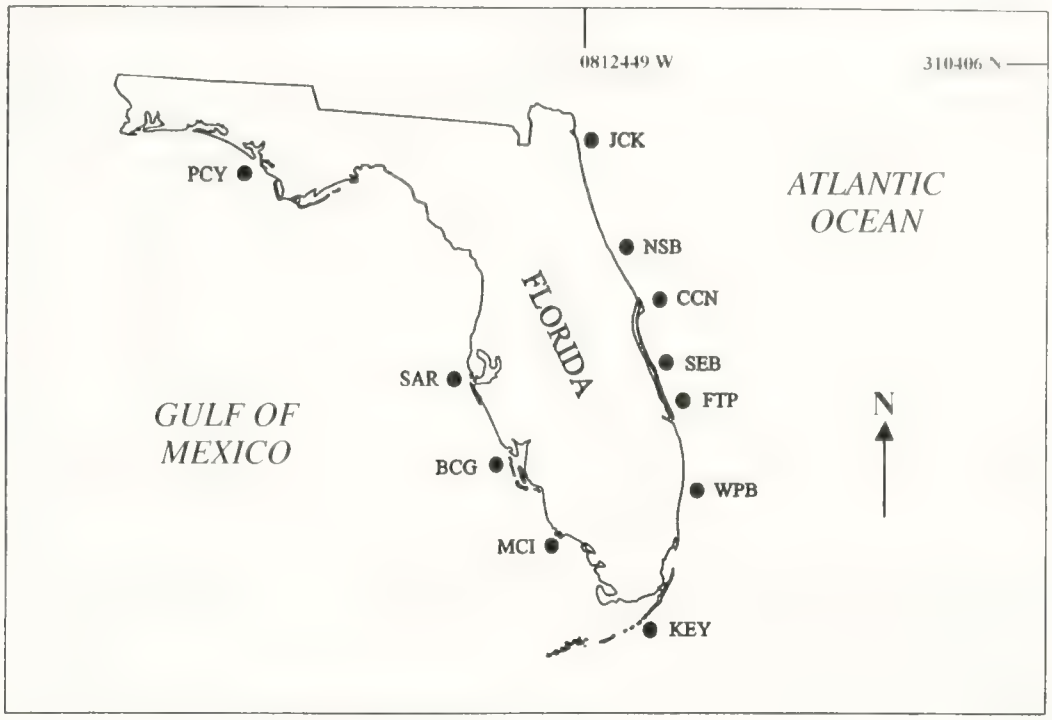

Figure 1

Sampling localities for king mackerel examined in the present study. Acronyms for sample localities are defined in Table 1.

of the distribution of genotypes at each microsatellite with the sex and age of individuals. Initial tests involved each of the 20 samples separately. We then pooled individuals sampled at Atlantic localities (nine samples), in the Florida Keys (three samples), at Gulf localities (eight samples), and over all localities (20 samples) in order to increase cell sizes in individual tests. Probability (P) values for these tests of independence were estimated by permutation (1000 resamplings) and significance levels for simultaneous tests were adjusted with the sequential Bonferroni approach.

Tests of genetic homogeneity among samples included exact tests, as implemented in GENEPOP, the Monte Carlo procedure of Roff and Bentzen (1989), as implemented in the restriction enzyme analysis package of McElroy et al. (1992), and the analysis of molecular variance (AMOVA) of Excoffier et al. (1992). Significance of tests of genetic homogeneity employed permutation with 1000 resamplings per individual comparison, and significance levels for simultaneous tests were adjusted by using the sequential Bonferroni approach. Tests of genetic homogeneity were carried out separately for each of the seven microsatellites. Individual tests were carried out 1) among all 20 samples, 2) among samples (nine) from Atlantic localities, 3) among samples (three) from the Florida Keys, and 4) among samples (eight) from Gulf localities. Analysis of molecular variance (AMOVA) was employed to generate estimates of (genetic) variance components and Φ statistics for the same comparisons. Φ statistics are a set of hierarchical F-statistic analogs that consider evolutionary distance among alleles. Significance of Φ statistics employed permutation (1000 resamplings).

Exact tests, the Monte Carlo procedure of Roff and Bentzen, and AMOVA also were used to assess genetic homogeneity 1) between samples from the Atlantic versus those from the Gulf (excluding samples from the Florida Keys), and 2) among samples from the Atlantic, the Florida Keys, and the Gulf. This design was chosen *a priori*, in part because it was geographically logical, in part because the southern Florida peninsula apparently serves (or has served) as a biogeographic boundary for a number of marine species (Avise, 1992; Gold and Richardson, 1998). The hierarchical capability of AMOVA also permitted a test of homogeneity among samples within the three regional groupings. We also carried out homogeneity testing to examine the temporal stock boundaries currently used in management planning for the king mackerel resource. Each of the 20 samples of king mackerel was designated as either Atlantic or Gulf stock according to the time of year during which they were sampled. Six of the samples thus were designated Atlantic stock and 14 of the samples were designated Gulf stock (Table 1). Genetic homogeneity was then tested between the Atlantic and Gulf "stocks," by using exact tests and the Monte Carlo procedure of Roff and Bentzen.

Clustering of genetic distances, spatial autocorrelation analysis, and assignment tests also were employed to assess temporal and spatial variation of microsatellites.

Table 2

Summary of variation in seven microsatellites among king mackerel (*Scomberomorus cavalla*) sampled from the east and west coasts of Florida and the Florida Keys.

Microsatellite	Repeat sequence	No. of alleles	Average heterozygosity ±SE	P_{HW}[1]
Sca-14	$(CA)_6$ TA $(CA)_{13}$	5	0.474 ±0.016	0/20
Sca-23	$(CA)_4$ AAC $(AG)_{12}$	24	0.803 ±0.105	4/20[2]
Sca-37	$(TG)_5$ AG $(TG)_4$ AG $(TG)_4$	9	0.509 ±0.014	0/20
Sca-44	$(CTCG)_2$ CTAT $(CTGT)_5$	8	0.677 ±0.014	0/20
Sca-49	$(TG)_{17}$	15	0.656 ±0.018	0/20
Sca-61	$(CA)_6$ TGTA $(CA)_8$	6	0.311 ±0.018	0/20
Sca-65	$(TG)_{14}$	24	0.798 ±0.016	0/20

[1] Proportion of samples where $P < 0.05$, after Bonferroni correction.

[2] Probability values for three samples (SEB[2], KEY[1], and SAR[4]) were 0.000. The probability value for SAR[1] was 0.006 (adjusted α was 0.003).

Cavalli-Sforza's chord distance (Cavalli-Sforza and Edwards, 1967), as implemented in the GENEDIST program in version 3.4 of the phylogenetic inference package (PHYLIP) of Felsenstein (1992), was used to estimate the degree of genetic divergence or similarity between pairs of samples; neighbor joining (Saitou and Nei, 1987), from the NEIGHBOR program in PHYLIP, was used to cluster the resulting genetic distance matrix. A consensus of 500 neighbor-joining topologies was constructed by using the CONSENSE program in PHYLIP. Spatial autocorrelation analysis was carried out to determine whether allele distributions at each microsatellite at any given sample locality were independent of allele distributions in adjacent localities. Briefly, autocorrelation coefficients (Moran's I values), generated as a function of geographic distance between pairs of sample localities, were used to summarize patterns of geographic variation of allele frequencies at each microsatellite. Positive autocorrelations between adjacent localities, with decreasing autocorrelation as geographic distance between localities increases, are generally interpreted as an isolation-by-distance effect (Sokal and Oden, 1978a). We employed the spatial autocorrelation analysis program (SAAP) of Wartenberg (1989) and followed procedures outlined in Sokal and Oden (1978a, 1978b). "Noise" was minimized by including only alleles that occurred 20 or more times in the data set. The first of two SAAP runs employed equal geographic distances between each of five distance classes; the second employed equal numbers of pairwise comparisons in each distance class. Finally, assignment tests (Paetkau et al., 1995, 1997) were used to "assign" individuals within each of the 20 samples to one of two regional (spatial) groupings, Atlantic or Gulf. The two groupings were employed largely as a result of homogeneity tests of allele distributions, where existence of the two spatial groupings was weakly supported. Assignment tests have a number of uses (Waser and Strobeck, 1998): in this case we were interested in the proportion of individuals within a sample that could be assigned to each regional group, in relation to the locality of the sample and the season in which it was procured. Assignment tests were carried out employing the "assignment calculator" software available at http:\\www.biology.ualberta.ca/jbruzusto/Doh.html.

Results and discussion

Allele frequencies at the seven microsatellites in each of the 20 samples are given in Appendix Tables 2 and 3; number of individuals assayed, heterozygosity (direct count) values, and probability of conformance to expected Hardy-Weinberg proportions per microsatellite per individual sample are given in Appendix Tables 4 and 5. Summary statistics are given in Table 2 and include 1) repeat sequence of the cloned allele, 2) number of alleles detected, 3) average (direct count) heterozygosity (±SE) observed among samples, and 4) results of tests of conformance of observed genotype proportions to expectations of Hardy-Weinberg equilibrium. Cloned alleles at the seven microsatellites included simple (*Sca-49*, *Sca-65*) and complex (*Sca-14*, *Sca-23*, *Sca-37*, *Sca-61*) dinucleotide repeats and one complex tetranucleotide repeat (*Sca-44*). All dinucleotide microsatellites included CA (or complementary TG) repeats, with the number of alleles per microsatellite ranging from five (*Sca-14*) to twenty-four (*Sca-23* and *Sca-65*). Direct count heterozygosity, averaged over the twenty samples, ranged from 0.311 ±0.018 (*Sca-61*) to 0.803 ±0.105 (*Sca-23*). These results indicate that the seven microsatellites assayed in king mackerel are typical of microsatellites found in other vertebrate organisms, including fishes (e.g. DeWoody and Avise, 2000; Turner et al., 1998; Gold et al., 2001).

After sequential Bonferroni correction (Rice, 1989), genotype proportions at six of the microsatellites in all twenty samples did not deviate significantly from proportions expected under Hardy-Weinberg equilibrium. Genotype proportions at *Sca-23* among three of the samples (SEB[2], KEY[1], and SAR[4]) differed significantly (P=0.000) from Hardy-Weinberg equilibrium expectations, and at a fourth sample (SAR[1]), the probability value of 0.006 was very close to the Bonferroni adjusted alpha of 0.003 (Appendix

Table 3

Probability of genotype equilibrium (pairwise comparisons) among seven microsatellite loci in king mackerel (*Scomberomorus cavalla*) sampled from the east and west coasts of Florida and the Florida Keys. Corrected α (for initial test) = 0.002.

Microsatellite	*Sca-14*	*Sca-23*	*Sca-37*	*Sca-44*	*Sca-49*	*Sca-61*	*Sca-65*
Sca-14	—	0.389	0.684	0.900	0.665	0.977	0.906
Sca-23		—	0.022	1.000	0.805	0.603	0.194
Sca-37			—	0.724	0.876	0.910	0.430
Sca-44				—	0.328	0.000	0.020
Sca-49					—	0.295	0.998
Sca-61						—	0.873
Sca-65							-

Table 4

Results of tests for spatial homogeneity in allele distribution of seven microsatellites among king mackerel (*Scomberomorus cavalla*) sampled from the east and west coasts of Florida and the Florida Keys. P_{EXACT} = probability based on Fisher's exact tests, with 1000 permutations. P_{RB} = probability based on 1000 bootstrapped replicates (after Roff and Bentzen 1989).

	All samples[1]		Atlantic localities[2]		Florida Keys[3]		Gulf localities[4]	
Test group	P_{EXACT}	P_{RB}	P_{EXACT}	P_{RB}	P_{EXACT}	P_{RB}	P_{EXACT}	P_{RB}
Microsatellite								
Sca-14	0.465	0.447	0.845	0.826	0.510	0.503	0.697	0.668
Sca-23	0.026	0.106	0.250	0.416	0.076	0.068	0.175	0.140
Sca-37	0.431	0.388	0.592	0.498	0.038	0.024	0.592	0.619
Sca-44	0.084	0.073	0.558	0.508	0.111	0.161	0.187	0.136
Sca-49	0.230	0.472	0.487	0.746	0.591	0.529	0.112	0.112
Sca-61	0.278	0.428	0.531	0.563	0.065	0.084	0.273	0.296
Sca-65	0.611	0.588	0.457	0.611	0.910	0.957	0.411	0.169

[1] "All" includes all twenty samples.

[2] Atlantic includes JKV[1]–JKV[2], NSB, CCN, SEB[1]–SEB[3], FTP, and WPB (nine samples total). For explanation of these geographic abbreviations see Table 1.

[3] Keys include KEY[1]–KEY[3] (three samples total).

[4] Gulf includes MCI, BCG, SAR[1]–SAR[5], and PCY (seven samples total).

Tables 4 and 5). F_{IS} values (after Weir and Cockerham, 1984) for these four samples were all positive, indicating a deficit of heterozygotes and the possible presence of a null allele. However, probability values for tests of Hardy-Weinberg equilibrium at *Sca-23* among the remaining 16 samples were nonsignificant and averaged (±SE) 0.385 ±0.076. Although the possibility of a null allele at *Sca-23* cannot be dismissed unequivocally, genotypes at *Sca-23* appear overall to be distributed in accordance with Hardy-Weinberg equilibrium expectation. Finally, tests of genotypic equilibrium between pairs of microsatellites (samples pooled) yielded only one significant value (*Sca-44* × *Sca-61*) following Bonferroni correction (Table 3). Probability values of tests involving these two microsatellites, i.e. *Sca-44* × *Sca-61*, carried out within each of the 20 samples were all nonsignificant and averaged (±SE) 0.338 ±0.067. Of the remaining (pairwise) tests carried out within samples (420 tests in all), only four significant probability values were obtained: *Sca-37* and *Sca-44* (CCN), *Sca-23* × *Sca-44* (PCY), *Sca-37* × *Sca-49* (BCG), and *Sca-23* × *Sca-44* (SEB[2]). These results indicate that genotypes at the seven microsatellites are independent and hence are not linked genetically.

Tests for independence of allele distributions at each of the seven microsatellites versus both sex and age of individuals were carried out 1) within each of the 20 samples, and 2) among individuals (pooled) sampled from the Atlantic, the Florida Keys, the Gulf, and overall. In tests for independence with sex, eight significant probability values (P<0.05) were found prior to Bonferroni correction for simultaneous tests (data available from first author). None of these, however, were significant after Bonferroni correc-

Table 5

Results of tests for spatial homogeneity in allele distribution of seven microsatellites between and among pooled samples of king mackerel (*Scomberomorus cavalla*) from the east and west coasts of Florida and the Florida Keys. P_{EXACT} = probability based on Fisher's exact tests, with 1000 permutations. P_{RB} = probability based on 1000 bootstrapped replicates (after Roff and Bentzen 1989). Φ_{CT} = estimate of population subdivision based on AMOVA; P is the probability that Φ_{CT} differs significantly from zero (5000 permutations).

	Comparison of Atlantic[1] with Gulf[2]				Comparison of Atlantic and Keys[3] and Gulf			
	P_{EXACT}	P_{RB}	Φ_{CT}	P	P_{EXACT}	P_{RB}	Φ_{CT}	P
Microsatellite								
Sca-14	0.009	0.006	0.005	0.010	0.020	0.029	0.004	0.031
Sca-23	0.010	0.007	0.001	0.125	0.026	0.081	0.000	0.256
Sca-37	0.426	0.443	−0.001	0.588	0.009	0.001	−0.001	0.794
Sca-44	0.060	0.056	0.004	0.023	0.008	0.004	0.003	0.024
Sca-49	0.506	0.491	−0.001	0.912	0.580	0.535	−0.001	0.707
Sca-61	0.391	0.382	0.001	0.169	0.520	0.689	−0.001	0.398
Sca-65	0.625	0.645	0.004	0.556	0.775	0.508	0.004	0.145

[1] Atlantic includes JKV[1]–JKV[2], NSB, CCN, SEB[1] - SEB[3], FTP, and WPB (nine samples total). For explanation of these geographic abbreviation, see Table 1.

[2] Gulf includes MCI, BCG, SAR[1]–SAR[5], and PCY (seven samples total).

[3] Keys includes KEY[1]–KEY[3] (three samples total).

tion. In addition, one would expect that eight of 162 tests would be significant by chance alone at $\alpha = 0.05$. Finally, only one of the significant probability values occurred in a pooled comparison (*Sca-49* in the test of individuals from the Atlantic), where larger sample sizes were expected to increase robustness of tests of independence. In tests for independence of allele distributions with the age (year class) of individuals, eight significant probability values ($P<0.05$) were found prior to Bonferroni correction for simultaneous tests (data available from first author), two of which (*Sca-23* in SAR[4] and *Sca-61* in SAR[4]) were significant after Bonferroni correction with the use of eight simultaneous tests per microsatellite to estimate adjusted α levels. In both instances, nonindependence appeared to stem from an elevated incidence of specific alleles: *Sca-23*19* occurred at a frequency of 36% in the 1989 year class, as opposed to other year classes where its frequency ranged from 0% to 15%; and similarly, *Sca61*12* occurred at a frequency of 25–30% in the 1986 and 1989 year classes, as opposed to a frequency of 0–10% in the other year classes. We suspect these are anomalous instances that do not reflect an age-related effect, in part because allele distributions at *Sca-23* and *Sca-61* were independent of year class in all other samples, and in part because allele distributions at all microsatellites were independent of year class in pooled comparisons, where larger sample sizes should increase robustness of tests of independence. We concluded that allelic variation at the seven microsatellites essentially is independent of variation in both sex and age (year class).

Spatial homogeneity in allele distributions at each microsatellite was tested 1) over all 20 samples, 2) among samples from the Atlantic, 3) among samples from the Florida Keys, and 4) among samples from the Gulf. Only three significant probability values were found prior to Bonferroni correction: the exact test at *Sca-23* in the comparison over all 20 samples, and both the exact test and the Roff-Bentzen procedure at *Sca-37* in the comparison among samples from the Florida Keys (Table 4). None of the probability values were significant after Bonferroni correction. Tests for spatial homogeneity 1) between pooled samples from the Atlantic versus pooled samples from the Gulf, and 2) among pooled samples from the Atlantic, Florida Keys, and Gulf, indicated that all three regional groupings differed genetically from one another (Table 5). For the comparison Atlantic versus Gulf, significant heterogeneity prior to Bonferroni correction was found at *Sca-14* (all three statistical approaches), *Sca-23* (exact test and the Roff-Bentzen procedure), and *Sca-44* (for the probability that $\Phi_{CT}>0$). Probability values for *Sca-14* and *Sca-23* were marginal in relation to the (initial) Bonferroni adjusted α of 0.007, whereas the probability that Φ_{CT} > zero at *Sca-44* was nonsignificant after Bonferroni correction (Table 5). For the comparison of Atlantic, Florida Keys, and Gulf samples, significant heterogeneity was found at *Sca-14* (all three statistical approaches) and *Sca23* (exact test only) before but not after Bonferroni correction; heterogeneity at *Sca-37* and *Sca-44* in the same comparison was significant both before and after Bonferroni correction in at least one of the three statistical approaches (Table 5). Frequency differences at *Sca-14*, *Sca-23*, and *Sca-44* among the three regional groupings are shown in Table 6 and indicate that small differences in frequency of several alleles at each microsatellite appear to account for observed heterogeneity among the pooled sample comparisons.

Table 6

Allele frequencies at *Sca 14* and *Sca 23* for king mackerel (*Scomberomorus cavalla*) from the Atlantic, Florida Keys, and Gulf. Allele numbers represent the size in base pairs of the fragment amplified.

Microsatellite (allele)	Atlantic	Florida Keys	Gulf
Sca-14			
91	0.017	0.004	0.006
93	0.053	0.058	0.034
95	0.670	0.667	0.735
97	0.233	0.240	0.200
99	0.029	0.031	0.027
Sca-23			
138	0.063	0.054	0.052
140	0.028	0.050	0.028
142	0.221	0.250	0.241
144	0.012	0.008	0.005
146	0.131	0.092	0.121
148	0.026	0.008	0.015
150	0.146	0.108	0.132
152	0.185	0.177	0.149
154	0.008	0.011	0.015
156	0.100	0.111	0.109
158	0.011	0.011	0.011
160	0.009	0.011	0.012
162	0.001	0.000	0.001
164	0.015	0.027	0.016
166	0.002	0.004	0.009
168	0.002	0.004	0.000
170	0.009	0.019	0.018
172	0.017	0.019	0.039
174	0.009	0.015	0.010
176	0.002	0.008	0.009
178	0.002	0.008	0.001
180	0.001	0.004	0.002
182	0.000	0.000	0.002
184	0.002	0.000	0.000
Sca44			
153	0.004	0.015	0.009
157	0.084	0.046	0.090
161	0.030	0.019	0.041
165	0.366	0.308	0.295
169	0.398	0.465	0.438
173	0.104	0.131	0.118
177	0.012	0.011	0.010
181	0.000	0.004	0.000

In general, results of the three approaches to homogeneity testing were fairly consistent, with one notable exception. At *Sca-37*, probability values from the exact test and the Roff-Bentzen procedure were 0.009 and 0.001 in the comparison of Atlantic, Florida Keys, and Gulf samples, respectively, whereas the probability that Φ_{CT} differed from zero was 0.794 (Table 5). We examined this discrepancy further by carrying out "V" tests of homogeneity (DeSalle et al. 1987) for each allele at *Sca-37*. Significant heterogeneity ($P<0.05$) was found only at *Sca-37*12*: this allele was found only in the March 1997 sample from the Florida Keys (KEY[2]), where it occurred at a frequency of 6.9% (Appendix Tables 2 and 3). Because there were far fewer alleles at *Sca-37* sampled from the Florida Keys (258) than from either the Atlantic (884) or Gulf (872), the disproportionate frequency of this allele within the Florida Keys likely accounts for the significance encountered in the exact test and the Roff-Bentzen procedure. Given the absence of this allele in two of the three samples from the Florida Keys, we do not believe the significant heterogeneity detected at *Sca-37* is meaningful biologically.

Although homogeneity testing of pooled samples indicated that samples from the Atlantic differed from samples from the Gulf at *Sca-14* and *Sca-23*, and that samples from the Florida Keys differed from the other two at *Sca-44*, the allele-frequency differences were small and accounted for only a fraction of the overall genetic variance. Results of AMOVA for the comparison of Atlantic with Gulf samples revealed that on average 99.74% of the total genetic variance at the seven microsatellites occurred within samples, as compared to only 0.19% between regions. For the comparison of Atlantic, Florida Keys, and Gulf samples, 99.78% of the genetic variance on average occurred within samples, whereas only 0.11% occurred among regions. For both comparisons, the proportion of the variation among samples within regions accounted for the remainder of the genetic variance, and for both comparisons, this proportion was small and statistically nonsignificant.

Finally, homogeneity tests were used to examine the temporal stock boundaries currently used in management of the king mackerel resource by classifying each of the 20 samples as either Atlantic or Gulf stock (Table 1). No significant heterogeneity at any of the seven microsatellites was found, providing no genetic evidence for existence of temporal boundaries dividing Atlantic and Gulf migratory units (stocks).

Neighbor joining of Cavalli-Sforza's chord distances between pairs of samples yielded little evidence of geographic structure among the 20 samples. With few exceptions, samples from the same or geographically proximate localities did not cluster together, and most nodes in the topology (available from the first author) were supported by well less than 50% of bootstrap proportions. Spatial autocorrelation (SAAP) analysis also indicated the absence of a relationship between allele frequency and geographic distance. Initially, SAAP analysis employed both equal geographic distances between each of five distance classes and equal numbers of pairwise comparisons in each distance class. Analysis involving equal geographic distances between distance classes generated an uneven number of pairwise comparisons among distance classes, i.e. 18, 14, 15, 5, and 3 pairwise comparisons in distance classes 1–5, respectively, resulting in a high variance in Moran's I values among alleles in distance classes 4 and 5. Accordingly, the analysis was restricted to equal numbers of pairwise

comparisons (eleven) in each distance class. A total of 50 alleles (five at *Sca-14*, sixteen at *Sca-23*, four at *Sca-37*, six at *Sca-44*, five at *Sca-49*, three at *Sca-61*, and eleven at *Sca-65*) was tested, resulting in 250 Moran's I values. Only 10 significant ($P<0.05$) Moran's I values were generated: one at *Sca-14* (positive in the third distance class); seven at *Sca-23* (two positive in the second distance class, four positive in the third distance class, and one negative in the fifth distance class); two at *Sca-37* (one negative in the fourth distance class and one positive in the fifth distance class), and one at *Sca-65* (negative in the fifth distance class). No significant Moran's I values were found at *Sca-44*, *Sca-49*, and *Sca-61*. Only one of the "significant" Moran's I values (a positive value for *Sca-23*22* in the third distance class) remained significant after Bonferroni correction. The general absence of spatial autocorrelation indicates that gene flow in king mackerel is consistent with expectations of an island model (*sensu* Wright, 1943) of population structure, meaning that there is roughly an equal probability of gene flow between any of the 20 sample localities.

Assignment tests generally were concordant with other analyses of king mackerel microsatellites in that fish from the Atlantic appeared to be weakly divergent genetically from fish in the Gulf. Each of the 20 samples included high proportions of both Atlantic and Gulf fish, and there appeared to be no strong geographic pattern in proportion of fish assigned to either Atlantic or Gulf groups (Table 7). On average, samples from the Atlantic contained more "Atlantic" fish (54%), whereas samples from the Gulf contained more "Gulf" fish (51.2%). The three samples from the Florida Keys, on average, contained more "Atlantic" fish (53.3%), but this finding is misleading because the proportion of "Atlantic" fish in the three samples from the Florida Keys ranged from 37.2% to 64.0% (Table 7). In addition, the estimated proportions of Atlantic versus Gulf fish in samples from the Florida Keys were not consistent with what might be predicted based on the time of sampling and the spatial-temporal boundaries used currently in king mackerel stock assessment. The KEY[1] and KEY[2] samples were obtained in March, a time when both would be considered Gulf stock, yet close to the temporal boundary (1 April) when they would be considered Atlantic stock. The estimated proportion of Gulf fish in these two samples was 62.8% (KEY[1]) and 41.4% (KEY[2]). Alternatively, the KEY[3] sample was obtained in January when king mackerel in the Florida Keys are considered Gulf stock. The estimated proportion of Gulf fish in the KEY[3] sample was 36.0%.

Table 7

Assignment (as percentage) of individuals from 20 samples of king mackerel (*Scomberomorus cavalla*) from the east and west coast of Florida and the Florida Keys to either "Atlantic" or "Gulf" group.

	Assigned group	
Sample	Atlantic	Gulf
Atlantic Ocean		
JCK[1]	51.8	48.2
JCK[2]	62.5	37.5
NSB	58.0	42.0
CCN	46.0	54.0
SEB[1]	58.0	42.0
SEB[2]	62.0	38.0
SEB[3]	52.0	48.0
FTP	53.6	46.4
WPB	41.8	58.2
Avg	54.0	46.0
Florida Keys		
KEY[1]	37.2	62.8
KEY[2]	58.6	41.4
KEY[3]	64.0	36.0
Avg.	53.3	46.7
Gulf of Mexico		
MCI	49.1	50.9
BCG	45.7	54.3
SAR[1]	46.8	53.2
SAR[2]	53.3	46.7
SAR[3]	53.6	46.4
SAR[4]	41.1	58.6
SAR	54.3	45.7
PCY	46.0	54.0
Avg	48.8	51.2

Synopsis and conclusions

Genetic data obtained in our study are compatible with the hypothesis that two, weakly differentiated "genetic" subpopulations of king mackerel exist in waters off Florida and that considerable, perhaps extensive, mixing occurs between them. King mackerel sampled from the Florida Keys cannot be assigned unequivocally to either "genetic" stock; all collections tested appeared to be mixtures, with approximately equal proportions of fish from the two "genetic" stocks. These results are not consistent with the current spatial-temporal boundaries employed in stock assessment and allocation of the king mackerel resource. Results are consistent with the hypothesis that considerable gene flow occurs among all of the localities sampled, and that differences in gene flow likely do not arise as a function of geographic distance. Similar findings were obtained by Gold et al. (1997) in their study of variation in king mackerel mitochondrial DNA. The genetic differences between king mackerel in the Atlantic versus those in the Gulf most likely stem from reduced gene flow (migration) between the Atlantic and Gulf in relation to gene flow (migration) along the Atlantic and Gulf coasts of peninsular Florida. This is consistent with the notion based on studies of other marine fishes (Avise et al., 1992; Gold and Richardson, 1998) that the southern Florida peninsula serves (or has served) as a biogeographic boundary.

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Appendix Table 1

Microsatellites employed for king mackerel (*Scomberomorus cavalla*)

Microsatellite	Primer sequence (5′ → 3′) (forward and reverse, respectively)	Length (base pairs)	Annealing temperature (°C)
Sca-14	ATT CCC CAA ACA ATA CAC AC AGT GGA CGA CCC ATT CTA C	93	56
Sca-23	AGC CCT CTT ACA ATC TGC TAC CC AAA CCT TTA AGG CCT CAA GTA AAG	146	58
Sca-37	GCG CCG TGA CTT TTT ATT GCT C CAA CAA TTA GTC GCA GCC CTA G	154	58
Sca-44	ATG GCC AAA TGG CAC ATA ATC A GGG CAG CTC CAT GGG TCT GAG T	169	58
Sca-49	AGA TGT GAC AAC AGT GGG ATG GCA GCA GTA ATA AAG	157	56
Sca-61	GGT ACT GTC GGG AGA ATG AGA T TGA ATT TTA TAT GGA GGG TCT G	228	56
Sca-65	AGC TGC TGC CAT GAT TTG TT TCC TCC ACT GCC CCT TTC TT	129	52

Appendix Table 2

Allele frequencies at microsatellites in king mackerel (*Scomberomorus cavalla*). Legend to samples: JKV[1] = Jacksonville, Florida (July 1996); JKV[2] = Jacksonville, Florida (July, 1998); NSB = New Smryna Beach, Florida (July 1996); CCN = Cape Canaveral, Florida (December 1998); SEB[1] = Sebastian, Florida (March 1997); SEB[2] = Sebastian, Florida (March 1998); SEB[3] = Sebastian, Florida (December 1998); FTP = Ft. Pierce, Florida (April 1996); WPB = West Palm Beach, Florida (May 1998); KEY[1] = Key West, Florida (March 1996).

	Sample									
Microsatellite (allele)[1]	JKV[1]	JKV[2]	NSB	CCN	SEB[1]	SEB[2]	SEB[3]	FTP	WPB	KEY[1]
Sca-14										
91	0.000	0.031	0.040	0.030	0.010	0.030	0.000	0.009	0.009	0.010
93	0.046	0.063	0.070	0.040	0.041	0.070	0.050	0.063	0.037	0.030
95	0.741	0.719	0.650	0.630	0.735	0.590	0.670	0.643	0.667	0.680
97	0.185	0.188	0.220	0.250	0.184	0.280	0.250	0.259	0.259	0.260
99	0.028	0.000	0.020	0.050	0.031	0.030	0.030	0.027	0.028	0.020
Sca-23										
138	0.046	0.016	0.060	0.080	0.090	0.030	0.060	0.091	0.073	0.029
140	0.019	0.032	0.030	0.050	0.020	0.000	0.060	0.027	0.018	0.039
142	0.231	0.210	0.120	0.250	0.230	0.230	0.210	0.236	0.264	0.265
144	0.009	0.016	0.000	0.020	0.020	0.000	0.010	0.018	0.018	0.000
146	0.102	0.129	0.140	0.100	0.140	0.170	0.140	0.127	0.136	0.147
148	0.019	0.048	0.030	0.000	0.060	0.010	0.010	0.036	0.027	0.020
150	0.176	0.161	0.140	0.180	0.120	0.190	0.100	0.155	0.100	0.088
152	0.241	0.177	0.180	0.120	0.180	0.280	0.150	0.145	0.191	0.098
154	0.009	0.016	0.000	0.010	0.010	0.000	0.000	0.018	0.009	0.020
156	0.111	0.113	0.130	0.110	0.060	0.050	0.140	0.064	0.091	0.118
158	0.019	0.016	0.020	0.020	0.000	0.000	0.010	0.000	0.018	0.020
160	0.000	0.016	0.020	0.000	0.010	0.010	0.030	0.000	0.000	0.000
162	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.009	0.000
164	0.009	0.016	0.030	0.010	0.000	0.030	0.020	0.009	0.009	0.039
166	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.009	0.000
168	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.009	0.000	0.010
170	0.009	0.016	0.010	0.020	0.000	0.000	0.010	0.018	0.000	0.039
172	0.000	0.016	0.060	0.010	0.030	0.000	0.010	0.018	0.009	0.029
174	0.000	0.000	0.020	0.000	0.010	0.000	0.010	0.018	0.018	0.010
176	0.000	0.000	0.000	0.010	0.010	0.000	0.000	0.000	0.000	0.010
178	0.000	0.000	0.000	0.000	0.000	0.000	0.020	0.000	0.000	0.010
180	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.009	0.000	0.010
182	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
184	0.000	0.000	0.000	0.010	0.010	0.000	0.000	0.000	0.000	0.000
Sca-37										
138	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
142	0.000	0.031	0.030	0.000	0.000	0.010	0.010	0.000	0.000	0.020
144	0.667	0.688	0.600	0.694	0.720	0.630	0.540	0.623	0.630	0.637
146	0.009	0.016	0.040	0.010	0.030	0.010	0.030	0.019	0.019	0.000
148	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
150	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000
152	0.009	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
154	0.296	0.266	0.320	0.286	0.240	0.330	0.400	0.330	0.286	0.333
156	0.019	0.000	0.000	0.010	0.010	0.020	0.020	0.028	0.010	0.010
Sca44										
153	0.000	0.000	0.000	0.010	0.000	0.000	0.010	0.018	0.000	0.020
157	0.066	0.078	0.110	0.120	0.060	0.080	0.090	0.098	0.056	0.069
161	0.038	0.047	0.030	0.020	0.030	0.040	0.010	0.027	0.037	0.020
165	0.387	0.469	0.390	0.300	0.390	0.310	0.290	0.420	0.370	0.275
169	0.396	0.281	0.380	0.420	0.410	0.470	0.500	0.357	0.333	0.471
173	0.104	0.109	0.090	0.110	0.100	0.090	0.070	0.071	0.194	0.147
177	0.009	0.016	0.000	0.020	0.010	0.010	0.030	0.009	0.009	0.000
181	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

continued

Appendix Table 2 (continued)

Microsatellite (allele)[1]	Sample									
	JKV[1]	JKV[2]	NSB	CCN	SEB[1]	SEB[2]	SEB[3]	FTP	WPB	KEY[1]
Sca-49										
139	0.009	0.000	0.000	0.000	0.000	0.000	0.010	0.009	0.000	0.000
141	0.046	0.109	0.060	0.000	0.043	0.020	0.020	0.036	0.037	0.067
143	0.009	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.011
145	0.546	0.547	0.490	0.590	0.435	0.690	0.580	0.518	0.481	0.533
147	0.167	0.203	0.150	0.130	0.207	0.100	0.170	0.188	0.167	0.178
149	0.019	0.031	0.060	0.030	0.033	0.030	0.030	0.018	0.046	0.000
151	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
153	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
155	0.009	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000
157	0.046	0.031	0.090	0.070	0.076	0.060	0.080	0.063	0.093	0.089
159	0.130	0.063	0.130	0.170	0.196	0.090	0.090	0.161	0.148	0.111
161	0.009	0.016	0.000	0.010	0.011	0.010	0.010	0.009	0.009	0.011
163	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.009	0.000
165	0.009	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.009	0.000
167	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000
Sca 61										
208	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
210	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010
224	0.083	0.078	0.100	0.041	0.071	0.102	0.130	0.074	0.046	0.088
226	0.139	0.063	0.050	0.112	0.061	0.071	0.090	0.065	0.083	0.137
228	0.769	0.859	0.850	0.847	0.857	0.827	0.780	0.861	0.861	0.765
230	0.009	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.009	0.000
Sca 65										
117	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010
123	0.380	0.422	0.360	0.430	0.440	0.350	0.360	0.384	0.464	0.438
125	0.028	0.047	0.040	0.050	0.030	0.080	0.040	0.063	0.036	0.063
127	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.009	0.000	0.010
129	0.065	0.016	0.130	0.060	0.080	0.090	0.130	0.036	0.036	0.073
131	0.037	0.094	0.030	0.030	0.020	0.000	0.030	0.018	0.000	0.042
133	0.000	0.000	0.000	0.000	0.020	0.000	0.000	0.009	0.009	0.000
135	0.241	0.219	0.200	0.170	0.150	0.280	0.200	0.223	0.209	0.219
137	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.009	0.000
139	0.000	0.000	0.000	0.010	0.010	0.010	0.000	0.018	0.018	0.000
141	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000
143	0.009	0.000	0.000	0.010	0.020	0.010	0.000	0.009	0.018	0.010
147	0.093	0.047	0.150	0.080	0.080	0.070	0.150	0.080	0.109	0.063
149	0.028	0.016	0.010	0.020	0.020	0.010	0.010	0.018	0.009	0.021
151	0.009	0.016	0.020	0.040	0.030	0.030	0.020	0.045	0.018	0.000
153	0.046	0.016	0.020	0.000	0.040	0.020	0.020	0.045	0.027	0.031
155	0.037	0.031	0.020	0.050	0.010	0.020	0.020	0.036	0.027	0.010
157	0.019	0.016	0.010	0.030	0.020	0.020	0.010	0.009	0.000	0.000
159	0.000	0.016	0.000	0.020	0.010	0.000	0.000	0.000	0.000	0.000
161	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
163	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010
165	0.000	0.016	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000
167	0.009	0.031	0.010	0.000	0.010	0.000	0.010	0.000	0.000	0.000
171	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

[1] Allele number represents size in base pairs of the fragment amplified.

Appendix Table 3

Allele frequencies at microsatellites in king mackerel (*Scomberomorus cavalla*). Legend to samples: KEY[2] = Key West, Florida (March 1997); KEY[3] = Key West, Florida (January 1999); MCI = Marco Island, Florida (April 1996); BCG = Boca Grande, Florida (April 1996); SAR[1] = Treasure Island, Florida (April 1996); SAR[2] = Treasure Island, Florida (November 1996); SAR[3] = Treasure Island, Florida (April 1997); SAR[4] = Treasure Island, Florida (April 1998); SAR[5] = Treasure Island, Florida (November 1998); PCY = Panama City, Florida (October 1996).

	Sample									
Microsatellite (allele)[1]	KEY[2]	KEY[3]	MCI	BCG	SAR[1]	SAR[2]	SAR[3]	SAR[4]	SAR[5]	PCY
Sca-14										
91	0.000	0.000	0.009	0.014	0.000	0.009	0.009	0.000	0.007	0.000
93	0.069	0.080	0.036	0.057	0.033	0.018	0.063	0.021	0.036	0.020
95	0.724	0.620	0.745	0.771	0.685	0.764	0.741	0.771	0.714	0.680
97	0.190	0.250	0.173	0.143	0.250	0.200	0.170	0.186	0.221	0.230
99	0.017	0.050	0.036	0.014	0.033	0.009	0.018	0.021	0.021	0.070
Sca 23										
138	0.086	0.060	0.018	0.057	0.096	0.033	0.027	0.036	0.096	0.060
140	0.017	0.080	0.027	0.029	0.032	0.017	0.027	0.043	0.029	0.020
142	0.224	0.250	0.309	0.257	0.266	0.217	0.200	0.239	0.250	0.200
144	0.017	0.010	0.000	0.000	0.000	0.000	0.018	0.000	0.000	0.020
146	0.069	0.050	0.145	0.171	0.064	0.183	0.118	0.109	0.103	0.080
148	0.000	0.000	0.018	0.000	0.032	0.008	0.009	0.029	0.007	0.010
150	0.121	0.120	0.155	0.043	0.160	0.108	0.173	0.130	0.132	0.130
152	0.207	0.240	0.136	0.157	0.117	0.142	0.164	0.174	0.176	0.110
154	0.000	0.010	0.000	0.029	0.011	0.017	0.009	0.007	0.022	0.030
156	0.086	0.120	0.045	0.157	0.117	0.117	0.127	0.109	0.096	0.130
158	0.017	0.000	0.000	0.000	0.021	0.008	0.027	0.007	0.000	0.030
160	0.052	0.000	0.027	0.014	0.000	0.033	0.000	0.014	0.000	0.010
162	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.007	0.000	0.000
164	0.034	0.010	0.000	0.029	0.000	0.033	0.018	0.014	0.022	0.010
166	0.017	0.000	0.009	0.014	0.000	0.000	0.009	0.007	0.000	0.040
168	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
170	0.000	0.010	0.027	0.014	0.011	0.025	0.009	0.014	0.015	0.030
172	0.017	0.010	0.036	0.014	0.064	0.025	0.036	0.036	0.037	0.060
174	0.017	0.020	0.018	0.000	0.000	0.017	0.009	0.007	0.015	0.010
176	0.000	0.010	0.027	0.014	0.000	0.000	0.009	0.007	0.000	0.020
178	0.017	0.000	0.000	0.000	0.011	0.000	0.000	0.000	0.000	0.000
180	0.000	0.000	0.000	0.000	0.000	0.017	0.000	0.000	0.000	0.000
182	0.000	0.000	0.000	0.000	0.000	0.000	0.009	0.007	0.000	0.000
184	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sca-37										
138	0.069	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
142	0.034	0.000	0.009	0.000	0.000	0.017	0.009	0.007	0.000	0.023
144	0.603	0.653	0.627	0.700	0.628	0.642	0.679	0.600	0.579	0.593
146	0.000	0.010	0.018	0.043	0.021	0.025	0.036	0.007	0.007	0.000
148	0.000	0.000	0.000	0.000	0.000	0.009	0.000	0.000	0.000	0.000
150	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
152	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
154	0.276	0.327	0.327	0.257	0.319	0.292	0.250	0.343	0.379	0.349
156	0.017	0.010	0.018	0.000	0.032	0.017	0.027	0.043	0.036	0.035
Sca-44										
153	0.034	0.000	0.009	0.014	0.000	0.017	0.000	0.029	0.000	0.000
157	0.069	0.010	0.056	0.100	0.096	0.133	0.089	0.114	0.072	0.050
161	0.052	0.000	0.037	0.014	0.032	0.008	0.098	0.036	0.051	0.040
165	0.276	0.360	0.259	0.314	0.255	0.300	0.268	0.293	0.355	0.300
169	0.431	0.480	0.546	0.443	0.436	0.408	0.455	0.393	0.413	0.430
173	0.121	0.120	0.093	0.100	0.170	0.133	0.080	0.129	0.087	0.160
177	0.017	0.020	0.000	0.014	0.011	0.000	0.009	0.007	0.022	0.020
181	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

continued

Appendix Table 3 (continued)

Microsatellite (allele)[1]	Sample									
	KEY[2]	KEY[3]	MCI	BCG	SAR[1]	SAR[2]	SAR[3]	SAR[4]	SAR[5]	PCY
Sca-49										
139	0.000	0.000	0.009	0.000	0.011	0.010	0.009	0.000	0.000	0.000
141	0.069	0.070	0.055	0.043	0.054	0.031	0.054	0.043	0.036	0.020
143	0.000	0.000	0.000	0.000	0.022	0.000	0.000	0.007	0.000	0.000
145	0.621	0.580	0.464	0.457	0.576	0.594	0.455	0.614	0.529	0.560
147	0.121	0.100	0.218	0.200	0.076	0.156	0.152	0.114	0.200	0.180
149	0.017	0.040	0.009	0.029	0.011	0.010	0.027	0.014	0.014	0.060
151	0.000	0.000	0.009	0.014	0.000	0.000	0.000	0.007	0.000	0.000
153	0.000	0.000	0.000	0.000	0.011	0.000	0.000	0.000	0.000	0.000
155	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
157	0.052	0.080	0.100	0.129	0.076	0.063	0.089	0.021	0.071	0.050
159	0.086	0.130	0.118	0.129	0.141	0.135	0.196	0.171	0.143	0.130
161	0.034	0.000	0.018	0.000	0.000	0.000	0.009	0.007	0.000	0.000
163	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
165	0.000	0.000	0.000	0.000	0.022	0.000	0.009	0.000	0.000	0.000
167	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.007	0.000
Sca-61										
208	0.000	0.000	0.000	0.000	0.000	0.009	0.000	0.000	0.000	0.000
210	0.000	0.000	0.000	0.000	0.011	0.000	0.000	0.000	0.000	0.000
224	0.052	0.130	0.073	0.086	0.054	0.138	0.127	0.107	0.100	0.070
226	0.017	0.100	0.055	0.143	0.098	0.078	0.100	0.114	0.121	0.070
228	0.931	0.760	0.873	0.757	0.837	0.776	0.755	0.779	0.771	0.860
230	0.999	0.010	0.000	0.014	0.000	0.000	0.018	0.000	0.007	0.000
Sca-65										
117	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010
123	0.483	0.460	0.364	0.357	0.436	0.446	0.375	0.357	0.386	0.340
125	0.017	0.030	0.036	0.100	0.064	0.045	0.071	0.086	0.043	0.060
127	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
129	0.052	0.080	0.055	0.057	0.032	0.054	0.063	0.057	0.021	0.060
131	0.000	0.020	0.027	0.000	0.064	0.036	0.018	0.071	0.029	0.020
133	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
135	0.207	0.160	0.273	0.300	0.245	0.179	0.205	0.193	0.243	0.190
137	0.000	0.000	0.000	0.000	0.000	0.009	0.000	0.000	0.000	0.010
139	0.000	0.010	0.000	0.000	0.000	0.009	0.009	0.007	0.007	0.000
141	0.000	0.000	0.018	0.000	0.000	0.000	0.000	0.000	0.000	0.010
143	0.017	0.010	0.000	0.014	0.000	0.036	0.009	0.000	0.007	0.000
147	0.103	0.110	0.073	0.029	0.053	0.080	0.080	0.100	0.114	0.090
149	0.034	0.020	0.036	0.057	0.021	0.000	0.018	0.014	0.029	0.020
151	0.017	0.040	0.055	0.000	0.000	0.009	0.018	0.014	0.021	0.040
153	0.034	0.030	0.018	0.029	0.021	0.036	0.054	0.029	0.029	0.090
155	0.017	0.020	0.018	0.014	0.032	0.027	0.045	0.021	0.029	0.050
157	0.017	0.010	0.018	0.014	0.011	0.018	0.027	0.014	0.029	0.010
159	0.000	0.000	0.000	0.014	0.000	0.000	0.009	0.014	0.000	0.000
161	0.000	0.000	0.009	0.000	0.000	0.000	0.000	0.007	0.000	0.000
163	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
165	0.000	0.000	0.000	0.000	0.000	0.018	0.000	0.000	0.000	0.000
167	0.000	0.000	0.000	0.014	0.021	0.000	0.000	0.014	0.007	0.000
171	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.007	0.000

[1] Allele number represents size in base pairs of the fragment amplified

Appendix Table 4

Summary statistics for each of seven microsatellites among samples of king mackerel (*Scomberomorus cavalla*): n = number of individuals assayed; H_{DC} = direct-count heterozygosity; and P_{HW} = probability that genotypes conform to expectations of Hardy-Weinberg equilibrium. Legends to sample localities are given in Appendix Table 2.

Microsatellite	JKV[1]	JKV[2]	NSB	CCN	SEB[1]	SEB[2]	SEB[3]	FTP	WPB	KEY[1]
Sca-14										
n	54	32	50	50	49	50	50	56	54	50
H_{DC}	0.481	0.375	0.460	0.500	0.408	0.600	0.420	0.571	0.537	0.520
P_{HW}	0.710	0.297	0.141	0.354	0.333	0.431	0.440	0.203	0.070	0.103
Sca-23										
n	54	31	50	50	50	50	50	55	55	51
H_{DC}	0.833	0.806	0.780	0.840	0.820	0.600	0.800	0.855	0.800	0.765
P_{HW}	0.571	0.094	0.121	0.618	0.654	0.000	0.141	0.085	0.483	0.000
Sca-37										
n	54	32	50	49	50	50	50	53	54	51
H_{DC}	0.500	0.531	0.540	0.449	0.380	0.520	0.560	0.585	0.463	0.608
P_{HW}	0.039	0.306	0.903	0.193	0.607	1.000	0.784	0.291	0.293	0.069
Sca-44										
n	53	32	50	50	50	50	50	56	54	51
H_{DC}	0.604	0.719	0.720	0.680	0.720	0.620	0.660	0.643	0.722	0.569
P_{HW}	0.584	0.965	0.911	0.518	0.583	0.618	0.719	0.875	0.095	0.095
Sca-49										
n	54	32	50	49	46	50	50	56	54	45
H_{DC}	0.611	0.656	0.820	0.680	0.739	0.540	0.620	0.696	0.704	0.600
P_{HW}	0.722	0.543	0.871	0.509	0.290	0.753	0.313	0.958	0.943	0.571
Sca-61										
n	54	32	50	49	49	49	50	54	54	51
H_{DC}	0.407	0.281	0.280	0.306	0.224	0.306	0.360	0.204	0.278	0.392
P_{HW}	1.000	1.000	0.709	1.000	0.152	0.306	0.703	0.093	1.000	0.851
Sca-65										
n	54	32	50	50	50	50	50	56	55	48
H_{DC}	0.870	0.813	0.900	0.900	0.820	0.800	0.780	0.839	0.727	0.729
P_{HW}	0.975	0.388	0.647	0.985	0.777	0.242	0.917	0.978	0.479	0.838

Appendix Table 5

Summary statistics for each of seven microsatellites among samples of king mackerel (*Scomberomorus cavalla*): n = number of individuals assayed; H_{DC} = direct-count heterozygosity; and P_{HW} = probability that genotypes conform to expectations of Hardy-Weinberg equilibrium. Legends to sample localities are in Appendix Table 2.

Microsatellite (allele)	KEY[2]	KEY[3]	MCI	BCG	SAR[1]	SAR[2]	SAR[3]	SAR[4]	SAR[5]	PCY
Sca-14										
n	29	50	55	35	46	55	56	70	70	50
H_{DC}	0.517	0.500	0.473	0.371	0.543	0.345	0.429	0.414	0.500	0.520
P_{HW}	0.760	0.143	0.246	0.042	0.562	0.403	0.690	0.540	0.824	0.336
Sca-23										
n	29	50	55	35	47	60	55	69	68	50
H_{DC}	0.897	0.760	0.745	0.886	0.723	0.800	0.855	0.783	0.838	0.880
P_{HW}	0.416	0.106	0.032	0.947	0.006	0.039	0.846	0.000	0.647	0.365
Sca-37										
n	29	50	55	35	47	60	55	69	68	50
H_{DC}	0.552	0.469	0.491	0.486	0.447	0.617	0.446	0.571	0.543	0.419
P_{HW}	0.092	0.647	0.384	0.851	0.079	0.431	0.817	0.499	0.785	0.235
Sca-44										
n	29	50	54	35	47	60	56	70	70	50
H_{DC}	0.828	0.560	0.611	0.686	0.723	0.633	0.696	0.714	0.739	0.700
P_{HW}	0.686	0.219	0.953	0.722	0.353	0.495	0.335	0.813	0.132	0.050
Sca-49										
n	29	50	55	35	46	48	56	70	70	50
H_{DC}	0.586	0.580	0.727	0.771	0.630	0.625	0.714	0.500	0.686	0.640
P_{HW}	0.667	0.055	0.679	0.153	0.098	0.806	0.303	0.246	0.847	0.856
Sca-61										
n	29	50	55	35	46	58	55	70	70	50
H_{DC}	0.138	0.480	0.218	0.343	0.326	0.379	0.327	0.314	0.371	0.280
P_{HW}	1.000	0.486	0.390	0.073	1.000	0.348	0.016	0.105	0.364	1.000
Sca-65										
n	29	50	55	35	47	56	56	70	70	50
H_{DC}	0.690	0.800	0.727	0.743	0.681	0.696	0.839	0.843	0.886	0.880
P_{HW}	0.581	0.656	0.317	0.615	0.250	0.425	0.526	0.879	0.183	0.942

Abstract—Catch rates in the South African rock lobster (*Jasus lalandii*) fishery declined after 1989 in response to reduced adult somatic growth rates and a consequent reduction in recruitment to the fishable population. Although spatial and temporal trends in adult growth are well described, little is known about how juvenile growth rates have been affected. In our study, growth rates of juvenile rock lobster on Cape Town harbor wall were compared with those recorded at the same site more than 25 years prior to our study, and with those on a nearby natural nursery reef. We found that indices of somatic growth measured during 1996–97 at the harbor wall had declined significantly since 1971–72. Furthermore, growth was slower among juvenile *J. lalandii* at the harbor wall than those at the natural nursery reef. These results suggest that growth rates of juvenile and adult *J. lalandii* exhibit similar types of spatiotemporal patterns. Thus, the recent coastwide decline in adult somatic growth rates might also encompass smaller size classes.

Do fluctuations in the somatic growth rate of rock lobster (*Jasus lalandii*) encompass all size classes? A re-assessment of juvenile growth

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The South African fishery for rock lobster (*Jasus lalandii*) began in the late nineteenth century and expanded rapidly so that catches peaked at approximately 10,000 metric tons (t) per annum between 1950 and 1965 (Pollock, 1986). However, subsequent deterioration in catches in the 1960s and 1970s was arrested only in the mid-1980s by the implementation of a management approach centered on an annual total allowable catch (TAC). Over the following five years, catches were maintained at apparently sustainable levels of 3500–4000 t per annum (Cockcroft and Payne, 1999), still representing the largest yield of any *Jasus* species at that time (Pollock, 1986). However, the period of stability ended after 1989, when catch rates declined in response to reduced adult somatic growth rates and a concomitant reduction in recruitment to that part of the population larger than the minimum legal size (Melville-Smith et al., 1995; Goosen and Cockcroft, 1995; Cockcroft, 1997).

Adult somatic growth rates for this resource are assessed by means of a tag-recapture program. This is relatively simple because mature individuals molt only once a year, just prior to the start of the commercial fishing season, and samples of these animals can be tagged shortly before they molt. Annual growth increments can therefore be calculated from postmolt-tagged animals recaptured during the subsequent commercial fishing season. This type of tag-recapture data is routinely collected from most of the fishing grounds that are important to the South African commercial fishery (Fig. 1, inset). This tagging program has yielded one of the most comprehensive rock lobster tagging-for-growth databases in the world; it contains continuous time-series for most areas since 1986 and broken time-series for some sites dating back to the 1969–70 season (Goosen and Cockcroft, 1995). Consequently, temporal and spatial trends in adult growth are well described (Melville-Smith et al., 1995; Goosen and Cockcroft, 1995; Cockcroft, 1997; Cruywagen, 1997; Pollock et al., 1997). By contrast, little is known about what may affect juvenile growth rates.

Of particular concern is the lack of information regarding the way in which juvenile growth rates might have been affected by factors that

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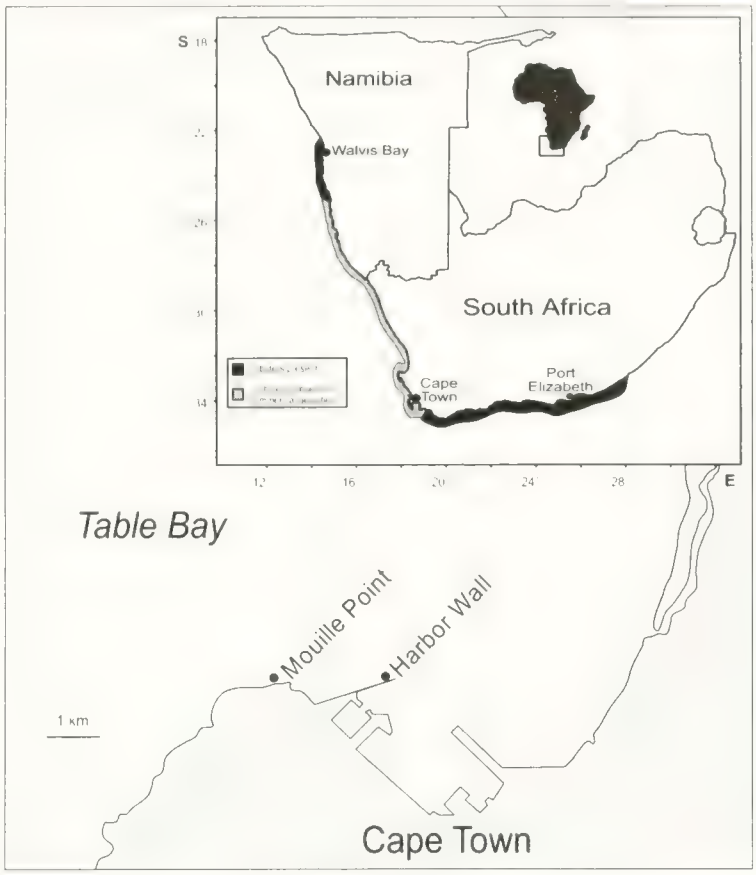

Figure 1

Map of Table Bay showing the position of the two study sites. Inset: map of southern Africa showing the distribution of rock lobster, *Jasus lalandii*.

caused the decline in adult growth rates during the early 1990s. A decrease in the size of females at 50% maturity provided indirect evidence that juvenile growth rates may also have been adversely affected (Pollock, 1987; Cockcroft and Goosen, 1995; Pollock, 1995; Pollock, 1997), but this decline in juvenile growth rates has not been confirmed by direct measurement.

Despite both this substantial gap in our knowledge of the ecology of *J. lalandii* and the growing international recognition of the importance of understanding the early life history stages of species with complex life cycles (Herrnkind et al., 1994), juvenile growth of this species was last assessed more than 25 years ago (Pollock, 1973). It was therefore essential that juvenile growth be re-examined by repeating Pollock's (1973) study at Cape Town harbor wall. This site was originally selected because of the large numbers of juvenile rock lobster present on the vertical face of the harbor wall and because these lobsters were easy to collect. In our study, a second, natural nursery reef site at nearby Mouille Point (Fig. 1) was selected to compare with the original artificial harbor wall site.

This paper addresses two hypotheses. The first is that somatic growth rates of juveniles on the harbor wall have not declined since Pollock's (1973) study. The second is that juvenile growth rates of rock lobster on the harbor wall are not different from those of rock lobster on the nearby natural nursery reef at Mouille Point.

Methods

Juvenile rock lobsters were collected between March 1996 and February 1997 at two sites: Cape Town harbor wall (seaward side) and Mouille Point (Fig. 1). Only the harbor wall was sampled in March and intervals between samples were approximately one month, although it was not possible to sample either site every month. Two autumn months (one for Mouille Point), two winter months, two spring months, and three summer months were sampled, thereby allowing for seasonal variation in growth.

Juvenile rock lobsters were sampled by two SCUBA divers who collected specimens for roughly 20–30 minutes, or by one diver for about twice as long (Table 1). At the harbor wall, divers started at the base of the wall (>10 m depth) and worked their way up to the surface, collecting every lobster encountered, where possible. At Mouille

Table 1

Summary of data relating to the field sampling of juvenile rock lobster at Mouille Point and Cape harbor wall, 1996–97.

Site	Sample date	Number of divers	Effort (diver minutes)	Water temperature[1] (°C)	Postmolt		Intermolt	Premolt		Total
					Soft new	Hard new	Hard	Hard old	Soft old	
Mouille Point	4 Apr 1996	1	40	11.2	2	4	202	65	0	273
	21 Jun 1996	1	50	13.5	2	3	167	67	0	239
	24 Jul 1996	2	30	13.3	8	15	174	56	0	253
	17 Oct 1996	2	75	12.5	2	10	239	80	4	335
	27 Nov 1996	2	50	9.4	4	12	291	58	0	365
	20 Dec 1996	1	40	10.0	4	14	212	60	1	291
	30 Jan 1997	2	50	8.8	2	19	224	52	0	297
	25 Feb 1997	2	65	9.2	5	17	176	77	0	275
Harbor wall	15 Mar 1996	1	60	10.0	12	6	325	121	0	464
	24 Apr 1996	2	55	12.5	3	7	228	52	0	290
	21 Jun 1996	1	20	13.5	1	1	210	42	2	256
	24 Jul 1996	1	45	13.3	8	13	243	29	6	299
	17 Oct 1996	2	60	12.5	3	15	205	80	0	303
	29 Nov 1996	2	45	12.9	4	9	262	30	0	305
	20 Dec 1996	1	40	10.0	6	7	275	38	0	326
	30 Jan 1997	2	50	8.8	2	13	280	38	2	335
	25 Feb 1997	2	64	9.2	10	34	210	76	0	330

[1] Temperature readings were taken from a temperature logger located in 10 m of water approximately 2 km east of Mouille Point

Point, divers swam around the reef area, covering different habitat types (ledges, vertical walls, cracks, etc.), and attempted to catch every lobster encountered.

The catch was maintained in a bin of seawater until the sex, shell state (*sensu* Pollock, 1973) and carapace length (CL) of each animal could be recorded. Hard old and soft old shell states were considered to represent premolt animals, soft new and hard new to represent postmolts, and those animals in the hard shell state were considered to be in the intermolt phase of the molt cycle. Postmolt and intermolt specimens were released, whereas premolt animals were measured to the nearest 0.1 mm and transported to the laboratory. Whenever relatively few premolt specimens of a particular size-category were captured during routine searches, additional dive time was spent collecting these. In the laboratory, captive specimens were transferred to perforated plastic jars (either 250 or 500 cm^3 in volume, with square perforations of approximately 25 mm^2), which were placed in a 2-m^3 holding tank. To mimic natural conditions (Table 1), aquarium water temperature was controlled between 11° and 14°C during holding, with a mean of 12.6°C (SD=0.48°C), and salinity was maintained at 35–36‰ by periodic addition of freshwater or partial replacement of seawater. Stocking density did not exceed three specimens per jar, and larger specimens were held singly or in pairs. By using a combination of jar number, sex, premolt carapace length, and the pattern of missing limbs, it was possible to identify each individual. Because *J. lalandii* are unable to feed shortly before molting (Zou-tendyk, 1988), it was assumed that no feeding was required. Jars were checked for molting individuals at least every second day. Cast exoskeletons were examined to identify those molting, and each new carapace length, as well as any limb regeneration, was recorded once the shell had hardened. Increment data recorded for December 1996 were discarded because of aquarium failure: raised temperatures and lower oxygen levels resulted in high mortality during molting. Because increments from specimens maintained in the laboratory for more than 18 days were considered unreliable, only animals that molted within this period were included in analyses.

Tests of the hypothesis that somatic growth rates of juveniles on the harbor wall had not declined since Pollock's (1973) study were complicated by the absence of his original data. All that remain are mean molt increments for male and for female specimens categorized into 5-mm-CL size classes, their standard deviations, and their sample sizes. Calculation of combined mean increments for males and females of a given size is simple, but their standard deviations had to be approximated by adding corresponding sums of squares for males and females and dividing this value by the overall degrees of freedom within the size class (Table 2). It had been our intention to compare these reconstructed data with those from our study by using a two-way ANOVA (site × size class), but this was not possible, given the limitations of Pollock's (1973) data. Instead, the data were subjected to a one-way ANOVA and subsequent Student-Newman-Keuls

Table 2

Mean molt increments and their standard deviations (mm CL) of juvenile *Jasus lalandii* measured on the harbor wall in 1971–72 and 1996–97, and at Mouille Point in 1996–97.

Size class (mm CL)	Harbor wall 1971–72[1]			Harbor wall 1996–97			Mouille Point 1996–97		
	n	Mean	SD[2]	*n*	Mean	SD	*n*	Mean	SD
15–20	14	2.65	0.76	35	1.94	0.56	21	2.10	0.46
20–25	37	3.12	0.82	98	2.45	0.56	74	2.72	0.64
25–30	28	3.71	1.08	95	2.78	0.64	80	2.93	0.68
30–35	14	4.36	0.73	64	3.07	0.75	93	2.86	0.96
35–40	17	4.71	0.54	33	3.39	0.93	44	3.56	0.90
40–45	23	4.72	0.93	13	3.66	0.93	29	3.74	0.77
45–50	23	5.02	0.62	6	3.50	0.79	3	4.00	0.69

[1] After Pollock (1973).

[2] An approximation of the standard deviation calculated by adding the sums of squares for males and females, and dividing by the overall degrees of freedom.

multiple range *post hoc* tests (SigmaStat, version 2.03, [SPSS Inc., 1997]). Of greatest interest in this analysis were the results of *post hoc* tests in which means of the corresponding size classes of the two sample periods were compared.

For comparison of length-related growth increments at the two sites in our study, individual molt increments were plotted against premolt carapace lengths, for each combination of sex and site, and their linear regressions were compared by using a two-way ANCOVA (Zar, 1984; Norman and Streiner, 1994).

Investigating relative intermolt periods from field samples requires identifying those specimens that are considered to be molting. Rock lobster juveniles in the hard old shell state (*sensu* Pollock [1973]) were easily identified as such by visual inspection, and we confirmed this by breaking the tip off an antenna and inspecting the condition of the underlying integument. Furthermore, on returning these specimens to the laboratory, they generally molted within 20 days. Because field samples were taken at intervals at least this long (Table 1), the proportion of each sample found to be in the hard old shell state was a reasonable indication of the relative number of juveniles molting during that sample month. This proportion, in turn, was used as a proxy for intermolt period under the assumption that shorter intermolt periods would result in relatively higher numbers of juveniles that were molting. The numbers of specimens with soft old or soft new shells did not accurately reflect the relative rate of molting because, as a result of behavioral modifications, rock lobster in these conditions may have had a lower catchability than those with hard shells.

Using this index of relative intermolt period, we performed a log-linear analysis (Zar, 1984; Norman and Streiner, 1994) to assess the interdependence of the factors site, size-category, sample month, and molt state with regard to the frequency of observations in each subcategory. Only size classes smaller than 40 mm carapace length were used in our analysis because the decreasing molt frequency with increasing carapace length means that larger sample sizes are required to accurately estimate the proportion of animals of the size class in which rock lobsters are molting in the population. However, the length distribution of juvenile lobsters meant that sample sizes decreased above 40 mm CL.

Results

An average of 323 juvenile *J. lalandii* was collected per sample at the harbor wall (256–464), and 291 at Mouille Point (239–365). After directed collections for additional premolt specimens of various sizes, a total of 375 juveniles from the harbor wall and 383 from Mouille Point were maintained in the laboratory for analysis of growth rates. Mortality rates were low (<1%) among these specimens, except during December 1996, when aquarium malfunction resulted in extensive fatalities during molting. Cannibalism was not observed during laboratory trials.

Individual molt increments amongst the captive specimens were highly variable, ranging from 0.4 to 5.5 mm. However, mean molt increments for each of seven consecutive 5-mm-CL size-intervals (Table 2) were consistently and significantly smaller in our study (1996–97 season) than those measured in 1971–72 (Table 3, Fig. 2). Thus, the hypothesis that somatic growth rates of juveniles on the harbor wall had not declined since Pollock's (1973) study could be rejected at one level. Unfortunately, there were no comparative data to provide accurate information on corresponding intermolt periods.

In terms of our samples from Mouille Point and the harbor wall, significant, positive linear relationships were found between molt increment and premolt carapace length for both males and females at both sites (Fig. 2,

Table 3

Results of one-way ANOVA comparing growth increments among size-intervals at the harbor wall from the two sample periods. Subsequent *post hoc* Student-Newman-Keuls multiple-range test results are summarized in the matrix below; an asterisk indicates that molt increments differ significantly ($P<0.05$) between the two samples being compared.

Source of variation	df	SS	MS	*F*	*P*
Between groups	13	332.57	25.58	48.1	<0.001
Within groups	486	258.48	0.53		
Total	499	591.06			

		1971–72							1996–97						
Size class (mm CL)		15–20	20–25	25–30	30–35	35–40	40–45	45–50	15–20	20–25	25–30	30–35	35–40	40–45	45–50
1971–72	15–20														
	20–25														
	25–30														
	30–35														
	35–40														
	40–45														
	45–50														
1996–97	15–20														
	20–25														
	25–30														
	30–35														
	35–40														
	40–45														
	45–50														

$P<0.0001$ in all cases). Three females at the harbor wall >50 mm CL were excluded from all analyses (unshaded circles, Fig. 2A) because they were the only specimens of this size. Further, females >50 mm CL might have had smaller than expected molt increments due to approaching maturity (Pollock, 1973).

Two-way, fixed effects ANCOVA comparing these linear regressions indicated no interaction between the factors site and sex; nor was there a significant sex-effect (Table 4). However, there was a significant site-effect: the relationship for samples from Mouille Point had a significantly higher regression constant than that for samples from the harbor wall (Table 4). These results imply first that there were no differences in length-specific growth increments between the sexes within sites. The second implication is that molt increment increased with carapace length at the same rate, irrespective of sex or site. Finally, juvenile lobsters of any given size or sex at Mouille Point grew significantly more during each molt stage than corresponding specimens at the harbor wall (see also Table 2 and Fig. 2).

Log-linear analysis indicated significant first-, second-, and third-order interactions among the factors site, size-category, sample month, and molt state (Table 5). However, the only significant third-order interaction was that among the independent factors site, size-category, and sample month. This interaction simply confirmed that size-frequency distributions differed between sites over the sample period, as would be expected if growth rates differed. Of the three remaining nonsignificant third-order interactions, the most important for our purposes were those including the site factor. These imply that the temporal pattern of molting is similar between sites, as is the size-specific pattern of molting. These results are supported by graphical representations of the data (Fig. 3), which suggest that for both sites 1) the proportion of molters per size-category decreases as size increases, and 2)

Table 4

Summary of ANCOVA results from length-specific molt increments classified according to sex and site.

Factor	df_{num}	df_{den}	*F*	*P*
Slope				
Site	1	597	0.70	0.40
Sex	1	597	0.66	0.42
Site × sex	3	595	0.61	0.61
Elevation				
Site	1	598	4.63	0.03
Sex	1	598	1.11	0.29
Site × sex	1	598	0.01	0.93

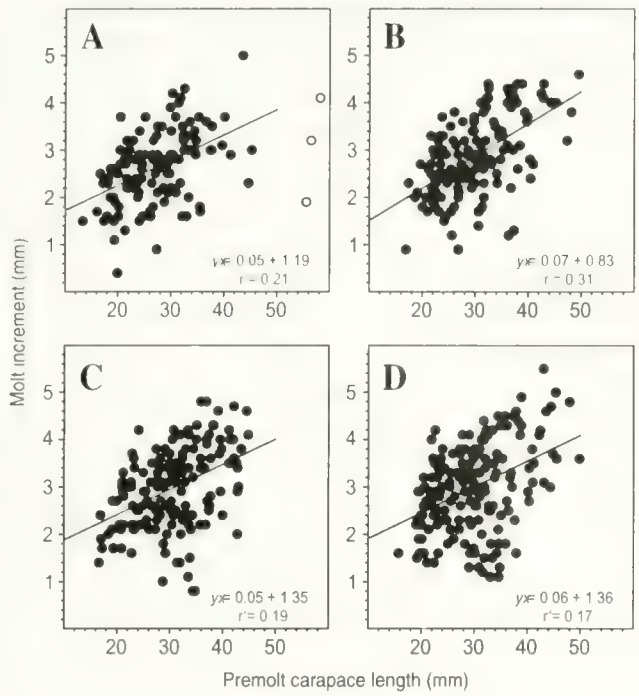

Figure 2

Relationship between molt increment and premolt carapace length of juvenile lobsters at the harbor wall and Mouille Point: (**A**) harbor wall females, (**B**) harbor wall males, (**C**) Mouille Point females, (**D**) Mouille Point males. Shaded circles represent data included in analyses; unshaded circles represent data excluded from analyses (see text for details).

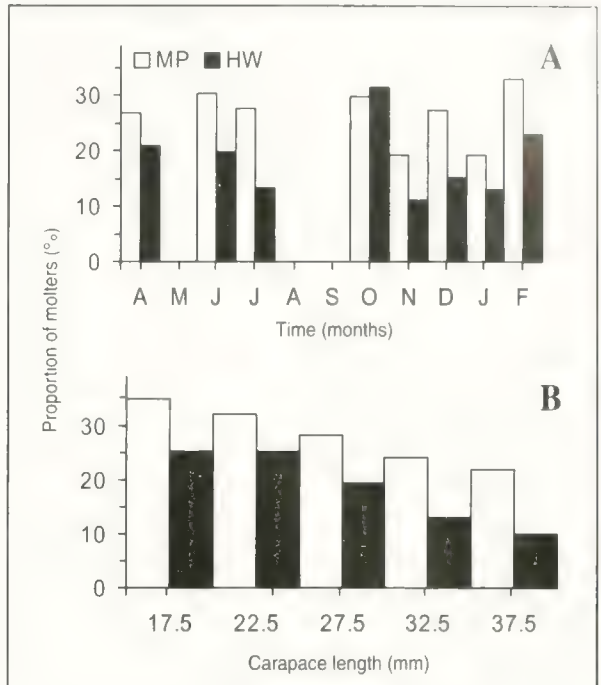

Figure 3

Site-specific patterns of the proportions of sampled juvenile rock lobster that were considered to be molting with respect to (**A**) sample month and (**B**) 5-mm-CL size classes. MP = Mouille Point; HW = harbor wall.

the proportion of lobsters in the molt state fluctuates over time. In both cases, the proportion of lobsters in the molt state was consistently lower at the harbor wall than at Mouille Point (with the exception of the sample taken in October 1996). This apparent dependence of molt state on each of the factors site, size-category, and sample date is confirmed by the corresponding significant second-order interactions (Table 5).

Together with the molt-increment data, these results give reason to reject the hypothesis that current juvenile growth rates on the harbor wall are no different from those on the nearby natural nursery reef in Mouille Point; growth is significantly faster at the latter.

Discussion

The significance of puerulus and postpuerulus ecology to the management of rock lobster fisheries is now widely accepted (Herrnkind et al., 1994). In the South African *J. lalandii* resource, the current controversy surrounding the question of whether or not temporal trends in juvenile growth rates reflect those of adults provides a good example of why so much emphasis should be placed on early life history stages. For this species, adult somatic growth rates have declined substantially since the mid-1980s (Melville-Smith et al., 1995; Cockcroft, 1997, Cockcroft and Payne, 1999). Although the causes of this phenomenon are not yet clearly understood, its widespread nature is indicative of a large-scale environmental perturbation. This has prompted hypotheses that the anomalous *El Niño* years of 1990–93 may have resulted in dramatic changes in the productivity of the southern Benguela Current (Pollock et al., 1997; Pollock et al., 2000). Alternatively, it is plausible that heavy, size-selective fishing of this resource may have caused a decline in growth rates by removing individuals genetically predisposed to more rapid growth (see for example Stokes and Law [2000]). Notwithstanding the causes, if it is incorrectly assumed that juvenile growth rates mirror the trends of the regularly monitored adults, overly conservative estimates of recruitment into the fishery might result, whereas assuming the converse could lead to a higher risk of overfishing.

Results from our re-examination of the growth rates of juvenile *J. lalandii* provided some evidence that temporal trends in their growth rates are consistent with those of the adults of the species. Specifically, juvenile molt increments at the Cape Town harbor wall were smaller in

Table 5

Results of log-linear analysis investigating the interdependence of the factors site (S), size-category (SC), sample month (M) and molt state (MS) with regard to the frequency of observations in each subcategory. χ^2 statistics are reported for conventional tests of observed versus expected frequencies and have been calculated for model fits with different numbers of levels of interactions as well as for partial and marginal associations among combinations of factors. In the latter sense, partial associations take into account the effect of all factors at each given level, whereas marginal associations take into account only those factors listed (Norman and Streiner, 1994).

Tests of hypotheses that all K-level interactions are simultaneously zero.

Level (K)	df	χ^2	P
1	13	1833.48	< 0.01
2	51	626.90	< 0.01
3	67	168.45	< 0.01
4	28	39.51	0.07

Tests of marginal and partial association

		Partial association		Marginal association	
Factor	df	χ^2	P	χ^2	P
Site (S)	1	6.60	0.01		
Size-category (SC)	4	500.95	< 0.01		
Sample month (M)	7	42.78	< 0.01		
Molt state (MS)	1	1198.48	< 0.01		
$S \times SC$	4	142.77	< 0.01	125.72	< 0.01
$S \times M$	7	23.89	< 0.01	21.05	< 0.01
$S \times MS$	1	52.47	< 0.01	35.73	< 0.01
$SC \times M$	28	320.55	< 0.01	307.70	< 0.01
$SC \times MS$	4	68.53	< 0.01	41.78	< 0.01
$M \times MS$	7	68.24	< 0.01	55.70	< 0.01
$S \times SC \times M$	28	121.80	< 0.01	129.12	< 0.01
$S \times SC \times MS$	4	7.99	0.09	4.91	0.30
$S \times M \times MS$	7	16.04	0.03	11.51	0.12
$SC \times M \times MS$	28	28.66	0.43	32.55	0.25

1996–97 than those recorded in 1971–72 (Pollock, 1973), irrespective of size. Although corresponding measures of intermolt period are not available, established trends in juvenile rock lobster biology indicate that such data would probably not have exhibited conflicting trends. In general, their growth rates tend to respond first by changes in molt frequency and then, under more extreme conditions, by changes in molt increments (Chittleborough, 1975; Serfling and Ford, 1975; Phillips et al., 1977; Dennis et al., 1997). Therefore, the trend to smaller growth increments among juvenile *J. lalandii* at the Cape Town harbor wall between 1971–72 and 1996–97 was most plausibly accompanied by an increase in intermolt period.

Adding credence to this deduction are Cockcroft and Goosen's (1995) results, which demonstrated that the size at which female *J. lalandii* reach sexual maturity on a range of fishing grounds had decreased significantly over the two decades leading up to the mid-1990s. Using simulation models, Pollock (1987) demonstrated that reduced juvenile growth rates would lead to a smaller size at sexual maturity. In combination, these conclusions provided additional rationale for rejecting the hypothesis that somatic growth rates of juvenile *J. lalandii* on the harbor wall have not declined since the last study.

Pollock (1973) found that a modal size of 38 mm CL was attained approximately 1.6 years after settling. This alone implies a slower growth rate than that for other temperate lobster species (Jernakoff et al., 1994). Because our data suggest that current growth rates are even slower than this, and that they may decline further with falling adult growth rates, recruitment to the fishable part of the *J. lalandii* resource must be seen as a real management concern (Bergh and Johnston, 1992). Therefore, the precautionary assumption made in the operational management procedure designed for this resource (Cockcroft and Payne, 1999; Pollock et al., 2000) that juvenile growth mirrors adult growth is justified.

Another feature of trends in growth rates shared between adult and juvenile *J. lalandii* is small-scale spatial variation. During the monitoring period, juveniles of this species grew relatively faster at Mouille Point than at the harbor wall, both in terms of molt increment

and intermolt period. Amongst adults, this variability has been attributed to patterns of food availability and gradients in environmental characteristics, particularly oxygen content (Newman and Pollock, 1974; Pollock and Beyers, 1981; Pollock, 1982; Pollock and Shannon, 1987; Pollock et al., 1997; Mayfield, 1998). Although there is some spatial separation of juvenile and adult *J. lalandii*, it is likely that the biotic structure of their environment influences juvenile growth rates in a manner similar to that of adults.

In a study of the diets of juvenile lobsters at the Cape Town harbor wall and Mouille Point, Mayfield (1998) found that diets were similar at the two sites, but that the benthic communities differed. He concluded that lobsters on the harbor wall would have to spend more time and energy feeding to maintain a diet similar to those at Mouille Point, where more favored food species (e.g. mussels, barnacles) were better represented. Similar patterns were evident when comparing diets of adults at Olifantsbos and Dassen Island (Mayfield, 1998), a slow- and fast-growth site, respectively (Cockcroft and Goosen, 1995). Subsequently, a more detailed study of the diets of two size classes (<35 mm CL and 40–60 mm CL) of juvenile *J. lalandii* at the Cape Town harbor wall and at Mouille Point was able to detect a significant difference between the diets of inhabitants of the two sites (Mayfield et al., 2000). Juveniles on the harbor wall consumed significantly less black mussel, their preferred prey species. This result, however, does not contradict the suggested link between food distribution and juvenile growth rates; specimens forced to subsist off suboptimal food resources could be expected to grow more slowly than those at liberty to pursue their preferred prey.

The differences in growth rates between juvenile *J. lalandii* at the artificial harbor wall and those at the natural nursery reef at Mouille Point do not necessarily preclude the use of the harbor wall as a legitimate site to continue monitoring juvenile growth. The existence of historical data (albeit for only two seasons) provides a good reference point, and the easy and consistent sampling conditions permit reliable data collection. These sampling conditions are of particular importance, given the established tendencies of early juveniles of other species of rock lobster on natural reefs to be less vulnerable to sampling than later stages (Annala and Bycroft, 1985; Marx and Herrnkind, 1985; Breen and Booth, 1989; Jernakoff, 1990; Childress and Herrnkind, 1994; Forcucci et al., 1994; Jernakoff et al., 1994). Furthermore, knowledge of how growth rates change over time is in itself important to the management of the fishery (Cockcroft, 1997).

Should spatial and temporal variability in juvenile growth continue to be a contentious issue, a juvenile tagging program would provide simpler and more rigorous comparisons. It might also provide reliable estimates of the intermolt period. Mitigating against this, however, are the low rate of recapture of tagged specimens in the wild and potential tag-related growth retardation and mortality. Nevertheless, continued monitoring of juvenile growth may elucidate how close this link is between adult and juvenile growth, thereby improving our ability to manage this valuable resource.

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Stock-rebuilding time isopleths and constant-*F* stock-rebuilding plans for overfished stocks

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Abstract—Stock-rebuilding time isopleths relate constant levels of fishing mortality (F), stock biomass, and management goals to rebuilding times for overfished stocks. We used simulation models with uncertainty about F_{MSY} and variability in annual intrinsic growth rates (r_y) to calculate rebuilding time isopleths for Georges Bank yellowtail flounder, *Limanda ferruginea*, and cowcod rockfish, *Sebastes levis*, in the Southern California Bight. Stock-rebuilding time distributions from stochastic models were variable and right-skewed, indicating that rebuilding may take less or substantially more time than expected. The probability of long rebuilding times increased with lower biomass, higher F, uncertainty about F_{MSY}, and autocorrelation in r_y values. Uncertainty about F_{MSY} had the greatest effect on rebuilding times. Median recovery times from simulations were insensitive to model assumptions about uncertainty and variability, suggesting that median recovery times should be considered in rebuilding plans. Isopleths calculated in previous studies by deterministic models approximate median, rather than mean, rebuilding times. Stochastic models allow managers to specify and evaluate the risk (measured as a probability) of not achieving a rebuilding goal according to schedule. Rebuilding time isopleths can be used for stocks with a range of life histories and can be based on any type of population dynamics model. They are directly applicable with constant F rebuilding plans but are also useful in other cases. We used new algorithms for simulating autocorrelated process errors from a gamma distribution and evaluated sensitivity to statistical distributions assumed for r_y. Uncertainty about current biomass and fishing mortality rates can be considered with rebuilding time isopleths in evaluating and designing constant-F rebuilding plans.

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Stock-rebuilding plans proposed for overfished stocks are best evaluated by stock-specific simulation analysis (e.g. PFMC[1]). However, general approaches are also valuable because many stocks are overfished (NMFS, 1999) and default or generic rebuilding plans can be used without extensive analyses for each species (e.g. PFMC[2]; Applegate et al.[3]). In this article we show how stock-rebuilding time isopleths can be used to design, evaluate, and monitor progress of "constant F" and other types of rebuilding plans. Constant-F stock-rebuilding plans maintain fishing mortality at a fixed level until the stock is rebuilt, and are relatively simple and easy to analyze. The isopleth approach is easy to use as both a general and stock-specific tool.

The U.S. Sustainable Fisheries Act (SFA) mandates rebuilding plans for overfished stocks (DOC, 1996, 1998). Federally managed stocks are considered overfished when stock biomass is less than the biomass threshold ($B_{Threshold}$) defined in the Fishery Management Plan (FMP). National Standard 1 (DOC, 1998) for the SFA indicates that $B_{Threshold}$ should be the greater of one-half of B_{MSY} (the theoretical biomass level for maximum sustained yield, MSY) or the minimum biomass from which rebuilding to B_{MSY} could be expected to occur within ten years if the stock is exploited at $F_{Threshold}$. Typically, $F_{Threshold} = F_{MSY}$ (the theoretical fishing mortality rate for MSY) when current biomass is at or above $B_{Threshold}$, and $F_{Threshold} < F_{MSY}$ at lower biomass levels. A common approach (Fig. 1, and Thompson, 1999) reduces $F_{Threshold}$ from the F_{MSY} level linearly to zero as biomass declines from $B_{Threshold}$. In cases where B_{MSY} and F_{MSY} can not be estimated, reasonable proxy values (e.g. one-half unfished biomass or $F_{0.1}$) are typically used instead.

The goal for most rebuilding plans under the SFA is to achieve the target biomass level (B_{MSY} or an acceptable proxy level) in ten years or less. Even with zero fishing mortality, ten years may not be sufficient to rebuild some overfished stocks. In such cases, the Guidelines for National Standard 1 allow a rebuilding time period no longer than one mean generation time (Restrepo et al., 1998) plus the expected time to recovery in the absence of fishing mortality (DOC, 1998).

[1] PFMC (Pacific Fishery Management Council). 1999. The coastal pelagic species fishery management plan, Amendment 8, 405 p. Pacific Fishery Management Council, 7700 NE Ambassador Place, Portland, OR, 97220-1384.

[2] PFMC (Pacific Fishery Management Council). 1999. Status of the Pacific Coast groundfish fishery through 1999 and recommended acceptable biological catch for 2000 stock assessment and fishery evaluation, 230 p. Pacific Fishery Management Council, 7700 NE Ambassador Place, Portland, OR, 97220-1384.

[3] Applegate, A., S. Cadrin, J. Hoenig, C. Moore, S. Murawski, and E. Pikitch. 1998. Evaluation of existing overfishing definitions and recommendations for new overfishing definitions to comply with the Sustainable Fisheries Act, 179 p. New England Fishery Management Council, 50 Water Street, Mill 2, Newburyport, MA 01950.

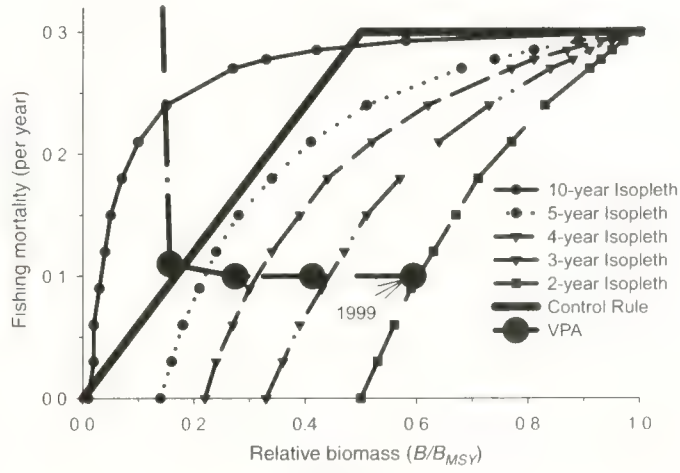

Figure 1

Isopleths for median rebuilding times based on a deterministic logistic population growth model (model type 1) for Georges Bank yellowtail flounder with F_{MSY}=0.3. Also shown are a common harvest control rule, and the biomass-F trajectory during 1996–99 for Georges Bank yellowtail flounder. The harvest control rule specifies a maximum (threshold) F as a function of stock biomass level. The biomass-F trajectory shows a time series of F and biomass estimates from virtual population analysis (VPA, Cadrin[5]).

Stock-rebuilding time isopleths

Cadrin (1999) calculated theoretical recovery times for Georges Bank yellowtail flounder (*Limanda ferruginea*) and used rebuilding time isopleths to depict trends in stock biomass in relation to fishing mortality. Calculations were based on a deterministic logistic population growth model with a range of constant annual fishing mortality rates ($\bar{F}$=zero to F_{MSY}) and a range of initial biomass levels less than the target level (B_0=zero to B_{MSY}). Recovery time was the number of years required for stock biomass to increase from an initial overfished biomass level ($B_0<B_{Threshold}$) to the biomass target $B_{Target}=B_{MSY}$, assuming a constant annual fishing mortality rate. Rebuilding time isopleths were formed by connecting points of initial biomass and constant fishing mortality (B_0, $\bar{F}_{B_0}$) with the same recovery time (Fig. 1). For example, beginning at the initial biomass level $B_0<B_{Target}$, any constant fishing mortality rate $\bar{F}_{B_0}$ on the 10-year isopleth would theoretically rebuild the stock to B_{Target} in ten years. In contrast, any constant-F value $<\bar{F}_{B_0}$ (below or to the right of the isopleth) would rebuild the stock sooner and any constant F values $>\bar{F}_{B_0}$ (above or to the left of the isopleth) would rebuild the stock later. Rebuilding time isopleths were used to develop overfishing definition options for nine overfished New England groundfish stocks (Applegate et al.[3]).

In this article, we calculate stock-rebuilding time isopleths based on stochastic population dynamics models and characterize statistical distributions (mean, median, and percentiles) of stock-rebuilding times under different assumptions about uncertainty and process error (process errors are uncertainty in population dynamics due to natural variability in growth, recruitment, and other biological factors, Hilborn and Walters, 1992). Like Cadrin (1999), we use logistic population growth models, but our analysis includes uncertainty about F_{MSY} and autocorrelated process errors in production. We analyze rebuilding times for two stocks (cowcod rockfish, *Sebastes levis*, and Georges Bank yellowtail flounder) with different life histories, levels of F_{MSY}, and autocorrelation in production process errors (the calculations are examples only and not for use by managers). We also describe how stock-rebuilding time isopleths from deterministic and stochastic models can be used to develop and evaluate rebuilding plans and to monitor their progress.

Materials and methods

Following Prager (1994), we used the continuous time version of the logistic population dynamic model in simulation calculations.[4] In particular, for the logistic population growth parameter r_y (subscripted to represent the value in year y) carrying capacity K, $b_y = r_y/K$, and $a_y = r_y - F_y \neq 0$:

$$B_{y+1} = \frac{a_y B_y e^{a_y}}{a_y + b_y B_y (e^{a_y} - 1)}. \quad (1)$$

[4] SAS simulation program code available from the senior author.

Table 1

Six types of simulation models used to estimate rebuilding time isopleths. Model types include all of the meaningful combinations of uncertainty about F_{MSY} and variance and autocorrelation in production process errors.

Model type	CV for uncertainty in F_{MSY} (%)	Variance in process errors (%)	Autocorrelation in process errors (ρ)	Description
1	Zero	0	zero	No uncertainty about F_{MSY}; deterministic production
2	20	0	zero	Uncertainty about F_{MSY}; deterministic production
3	Zero	from stock assessment	zero	No uncertainty about F_{MSY}; stochastic production; no autocorrelation
4	20	from stock assessment	zero	Uncertainty about F_{MSY}; stochastic production; no autocorrelation
5	Zero	from stock assessment	from stock assessment	No uncertainty about F_{MSY}; stochastic production; with autocorrelation
6	20	From stock assessment	from stock assessment	Uncertainty about F_{MSY}; stochastic production; with autocorrelation

When fishing and the intrinsic rate of increase exactly balance ($a_y = r_y - F_y = 0$):

$$B_{y+1} = \frac{B_y}{1 + b_y B_y}. \quad (2)$$

Note that biomass declines ($B_{y+1} < B_y$) when $r_y - F_y = 0$ because r_y is a maximum value defined in the limit as biomass approaches zero (Eq. 1).

Following Beddington and May (1977) and May et al. (1978), natural variation in population growth rates was included in our analysis by adding process errors to simulated r_y values. We hypothesized that the intrinsic rate of population increase was more important than carrying capacity in simulating population growth rates at low biomass levels, and in rebuilding overfished stocks. We focused on stochastic variation in r_y because it likely varies annually (e.g. due to variation in recruitment and growth). We could hypothesize reasonable lower bounds which included negative values; and variability in r_y could be reasonably described in statistical terms (e.g. mean, variance, and autocorrelation) based on available data. Carrying capacity (K) was assumed constant over time because no information about potential covariance in r_y and K was available.

In the deterministic logistic population model, $F_{MSY} = r/2$ and $B_{MSY} = K/2$ (Schaefer, 1954). For the sake of simplicity, we assumed $K=1$ so that $B_{Target} = B_{MSY} = 0.5$ and biomass B_y was measured in relation to K (e.g. $B_y = K = 1$ at carrying capacity). It was useful to express biomass in relation to K because estimates of ratios like B_t/B_{MSY} ($=2B_t/K$) are often more precisely estimated than either biomass B_y or carrying capacity K (Prager, 1994) and because the approach makes results easier to apply to other stocks.

We used six types of logistic population growth models (Table 1) based on a wide range of initial biomass (B_0), two levels of uncertainty about F_{MSY}, variance in process errors (stock dependent), and autocorrelation in process errors (also stock dependent). The number of years (an integer) required for the stock to rebuild to $0.95B_{MSY}$ was recorded in each simulation run. Recovery in the simulation model was at $0.95B_{MSY}$, rather than B_{MSY}, because biomass in the deterministic logistic production model at $F=F_{MSY}$ approaches asymptotically (but never reaches) B_{MSY} (this convention had negligible effect on results). Stochastic simulation model results were derived from 2000 individual model runs (the maximum length of each run was 2000 years) starting from each point in a grid of 31 values of F (i.e. 0, $F_{MSY}/30$, $2F_{MSY}/30$, ..., $29F_{MSY}/30$, F_{MSY}) and 35 values of initial biomass (i.e. $B_0 = 0$, $\delta \times 10^{-3}$, $\delta \times 10^{-2}$, $\delta \times 10^{-1}$, δ, 2δ, ..., 30δ, where $\delta = 0.9999 \times 0.95 \times B_{MSY}/K/30$).

We calculated distributional statistics including the mean, median ($Q_{50\%}$), and various quantiles (e.g. $Q_{90\%}$ for the ninety-percent quantile) for recovery times from all runs at each point in the grid of F and initial biomass levels. We then plotted isopleths (contours) for the distributional statistics. For example, to produce 10-year median rebuilding time isopleths, we calculated median recovery times for each point in the grid of F and initial biomass, and then drew contours (isopleths) by connecting points with 10 year median rebuilding times to identify fishing mortality rates that, if held constant, would give a 50% probability of rebuilding from the initial biomass to the target in ten years. We smoothed the isopleths in plots by using LOESS (locally weighted regression smoothing) regression (Cleveland and Devlin, 1988; Cleveland et al., 1988) to remove variation caused by the contouring algorithm and coarse grid of fishing mortality and biomass starting points.

Uncertainty

Uncertainty in estimates of F_{MSY} is likely larger than typically measured by variance estimates in assessment models because uncertainties in catch, the assumed natural mortality rate, somatic growth, and other factors are generally not included in stock assessment model variance calculations. In simulation runs including uncertainty, we used

$$F_{MSY,s} = \hat{F}_{MSY} + \varepsilon_s, \quad (3)$$

where $F_{MSY,s}$ was used in simulation s, $\hat{F}_{MSY}$ was the "best" estimate, and ε_s was drawn from a normal distribution with mean zero and variance $\sigma_\varepsilon^2 = CV^2 \hat{F}_{MSY}^2$. The CV (20%) assumed in our simulation runs implies that the true F_{MSY} is within ±40% of the best estimate with about 95% probability. We truncated $F_{MSY,r}$ values at ±50% $\hat{F}_{MSY}$ to avoid implausibly small (including negative) or large $F_{MSY,r}$ values. These *ad hoc* bounds seemed reasonable because they were slightly larger than the 95% confidence interval implied by the CV for uncertainty (±40%).

Our assumptions about uncertainty in F_{MSY} are crude but seem reasonable based on our experience and by analogy to uncertainty about natural mortality rates (M), which are sometimes used as a proxy for F_{MSY} (Clark, 1991). In assessment work, a stock with an assumed natural mortality rate M=0.2/yr, for example, might have a "subjective" uncertainty range of about ±40% (i.e 0.12–0.28/yr). It seems reasonable to assume that uncertainty about M and F_{MSY} would be similar.

Process errors

We modeled process errors as potentially autocorrelated random changes in the intrinsic population growth parameter (r_y). Previous analyses used independent or autocorrelated random errors in realized annual production rates (dB_y/dy, Sissenwine, 1977; Gleit, 1978; Shepherd and Horwood, 1980; Ludwig, 1981; Sissenwine et al., 1988), or independent random errors in recruitment (e.g. Getz, 1984), next year's biomass (B_{t+1}, Ludwig et al., 1988), or surplus production (Doubleday, 1976). Production process errors may be independent in some cases but were autocorrelated for both of our example stocks (see "Results" section).

Our analysis, like Sissenwine et al.'s (1988), includes autocorrelated errors because they affected rebuilding times in preliminary model runs, are biologically plausible and widely recognized (favorable and unfavorable conditions for production seem to persist for more than one year in many stocks), and because correlated errors were obvious in production model fits for Georges Bank yellowtail flounder and cowcod rockfish. In contrast to previous studies, we estimated variances and autocorrelations for stochastic r_y values in our simulation models from available data. In addition, our simulation models used lower bounds for r_y based on the natural mortality rate.

We used the gamma distribution (Johnson et al., 1994, Appendix 1) to describe process errors in the production model because it is flexible, asymmetrical (like our estimates of production process errors for cowcod rockfish), and (in the three-parameter form) accommodates negative r_y values. We devised a simple way to simulate autocorrelated process errors from a distribution nearly identical to a gamma distribution used to simulate uncorrelated process errors. This makes comparisons between runs with and without autocorrelation easier. Sissenwine et al. (1988) also used a gamma distribution for production process errors because simulated state variables in logistic models (with constant catch and Gaussian process errors on the realized production rate dB_y/dy) have distributions that resemble a gamma distribution (Dennis and Patil, 1984).

The first step in modeling production process errors was to obtain empirical estimates of variance and autocorrelation. Based on stock assessment results, surplus production in each year (P_y) was computed with the following equation:

$$P_{y-1} = B_{y-1} - B_y + C_y, \quad (4)$$

where C_y = catch data was catch; and
B_y = estimated biomass at the beginning of year y.

The discrete time version of our logistic model with process errors is

$$P_y = r_y B_y \left(1 - \frac{B_y}{K}\right). \quad (5)$$

Solving for r_y gives

$$r_y = \frac{P_y K}{B_y (K - B_y)}, \quad (6)$$

where B_y should be no larger than, say, 95% K to avoid unrealistic values of r_y that are calculated when positive production is observed in stock assessment results at biomass levels near or above estimates of K. As shown in the "Results" section, empirical estimates of variance σ^2 and autocorrelation (ρ) for r_y values were relatively insensitive to assumptions about K. The variance of observed r_y values includes both process and measurement errors and is an upper bound estimate for the variance due to process errors only. In other words, results of our simulation analyses may overstate the importance of production process errors in rebuilding overfished stocks because our variance estimates may be too large.

We used $-M$ (where M is the instantaneous natural mortality rate assumed in the stock assessment) as a lower bound on r_y in simulations. Negative r_y values are common in some stocks (e.g. 36% and 17% of years for anchovies [*Engraulis* spp.] and sardines [*Sardinops* and *Sardina* spp.], Jacobson et al., 2001) because stocks can decrease in biomass from one year to next with no fishing and because negative values are occasionally seen in real data sets (e.g. Myers et al., 1999). If process errors are ignored and M is constant, then

Table 2

Summary statistics and gamma distribution parameters for annual process errors in the intrinsic population growth rate (r_y) for Georges Bank yellowtail flounder (*Limanda ferruginea*), estimated from stock assessment results (Cadrin[5] in the main text). Parameters α and β were estimated with fixed $\gamma = -M$ by maximum likelihood. According to Cadrin,[5] the carrying capacity is K=99,000 metric tons (t) (95% confidence interval 84,500–103,000 t).

Parameter	K=84,500 t	K=99,400 t	K=103,000 t
Number B_y values <95% K	25	25	25
Sample mean	0.58	0.65	0.58
Sample variance	0.036	0.037	0.036
Autocorrelation ρ	0.34	0.33	0.34
α	15.7	17.5	15.7
β	0.0498	0.0488	0.0499
$\gamma = -M$	–0.2	–0.2	–0.2
Mean	0.58	0.65	0.58
Variance	0.039	0.039	0.039
Mode	0.53	0.61	0.53

$$r_y = G_y + R_y - M \quad (7)$$

where G_y = the instantaneous rate of somatic growth; and
R_y = an instantaneous rate for recruitment (in units of biomass).

Somatic growth and recruitment may be density dependent but are usually positive ($G_y \geq 0$ and $R_y \geq 0$). Thus, $r_y = -M$ is possible in the extreme case of zero growth and zero recruitment.

Production process errors were simulated by drawing random numbers from a three-parameter gamma probability distribution (Johnson et al., 1994, Appendix 1). Runs with autocorrelated process errors used one of two algorithms based on gamma distributions with adjusted parameter estimates (Appendix 2).

Georges Bank yellowtail flounder

Cadrin[5] used virtual population analysis (VPA, calibrated by using survey data) to estimate stock biomass for Georges Bank yellowtail flounder during 1973–98. In the same assessment, a surplus production model (ASPIC [stock-production model incorporating covariates], Prager, 1994) was used to estimate K=93,700 metric tons (t) (80% bootstrap confidence interval 87,700–97,000 t) and F_{MSY}=0.30/yr (80% bootstrap confidence interval 0.27–0.32/yr).

Cadrin's stock assessment[5] and our production calculations indicate that Georges Bank yellowtail flounder is a moderately long-lived (maximum observed age 14 yr, assumed M=0.2 /yr), relatively productive ($\bar{r}$=0.58–0.65) stock with some autocorrelation (ρ=0.33–0.34) in production process errors (Table 2). Empirical, and gamma distributions fit by maximum likelihood and the method of moments had similar means and variances (Table 2). Surplus production and biomass are related for Georges Bank yellowtail flounder, with P_y reduced at the low B_y levels (Fig. 2A). Variability in estimated r_y values indicate autocorrelation in process errors (Fig. 2B). The distribution of r_y values (Fig. 2C) was skewed to the left and there were no negative values. Gamma distributions fitted by maximum likelihood and the method of moments (Appendix 1) were similar in shape (Fig. 2C). In simulations for yellowtail flounder, we used F_{MSY}=0.30 (from ASPIC) with $\sigma^2_{r_y}$=0.037 and ρ=0.33.

Cowcod rockfish

Butler et al.[6] (see also Butler et al.[7]) estimated K=3400 t (95% CI 2800–4000 t) with a delay-difference biomass dynamic model for cowcod rockfish in the Southern California Bight. Annual biomass estimates from the same source were used to calculate surplus production during 1951–97 when the stock was fished down from about 3200 t to 240 t (about 7% of virgin biomass).

Butler et al.[6] and our production calculations indicate that cowcod rockfish are a long-lived (maximum observed

[5] Cadrin, S. X. 2000. Georges Bank yellowtail flounder. *In* Northern demersal working group: assessment of 11 northeast groundfish stocks through 1999. *In* Northeast Fisheries Science Center Reference Document 00-05, p. 45–64. Northeast Fisheries Science Center 166 Water Street, Woods Hole, MA, 02543.

[6] Butler, J. L., L. D. Jacobson, J. T. Barnes, and H. G. Moser. 2002. Manuscript in revew. Biology and population dynamics of cowcod rockfish (*Sebastes levis*) in the southern California Bight.

[7] Butler, J. L., L. D. Jacobson, J. T. Barnes, H. G. Moser, and R. Collins. 1999. Stock assessment of cowcod. *In* Appendix to the state of the Pacific Coast groundfish fishery through 1999 and recommended acceptable biological catch for 2000 stock assessment and fishery evaluation, p. Vi–113 (section 5). Pacific Fishery Management Council, 7700 NE Ambassador Place, Portland, OR, 97220-1384.

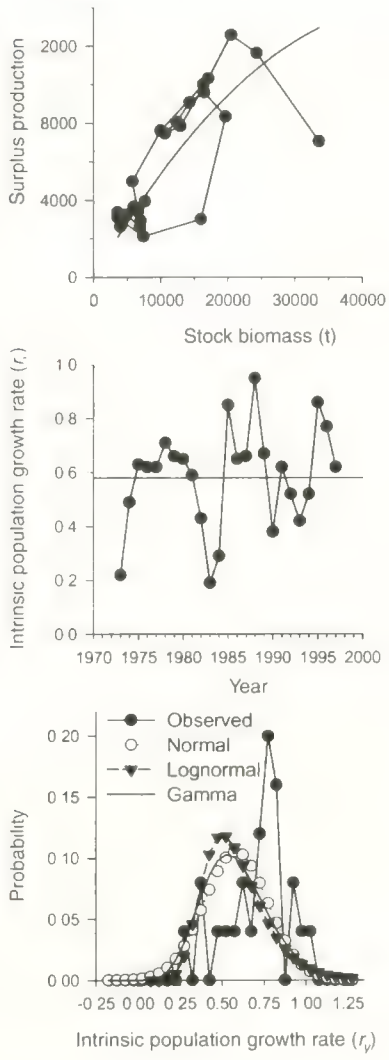

Figure 2

(**A**) Surplus production estimates P_y and biomass estimates B_y for Georges Bank yellowtail flounder during 1973–97. The biomass estimates and parabolic curve fitted to production estimates are from Cadrin.[5] (**B**) Time series of annual intrinsic rate of growth (r_y) parameter value estimates from Equation 6. (**C**) Probability distributions for r_y values used in simulations for Georges Bank yellowtail flounder.

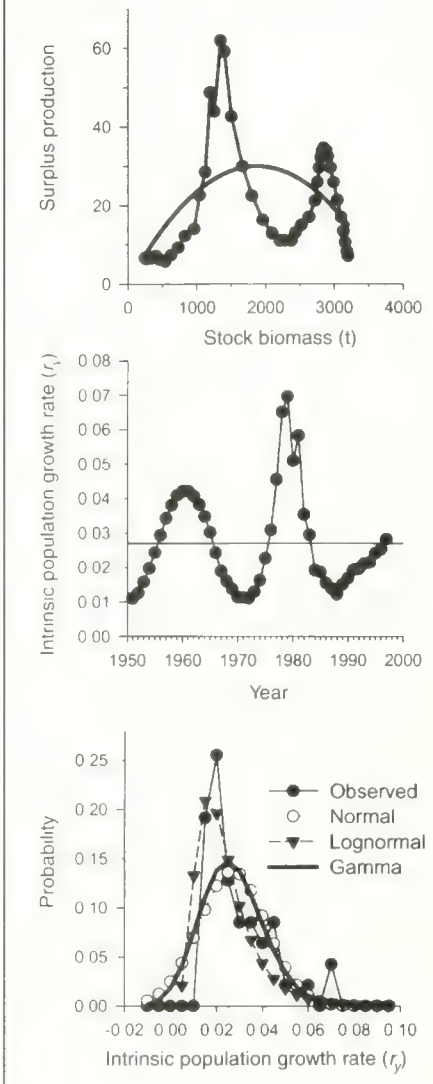

Figure 3

(**A**) Surplus production estimates P_y and biomass estimates B_y from Butler et al.[6] for cowcod rockfish during 1951–97 in the Southern California Bight. The parabolic curve fitted to production estimates (P_y) shows trends only and is not recommended for management purposes. (**B**) Time series of annual intrinsic rate of growth (r_y) parameter value estimates from Equation 6. (**C**) Probability distributions for r_y values used in simulations for cowcod rockfish.

age 55 yr, assumed M=0.055/yr), relatively unproductive stock ($\bar{r}_y$=0.027–0.037). Cowcod rockfish are much less productive than Georges Bank yellowtail flounder because of their long lives and slower growth and because adult habitat is limited to steep rocky areas in relatively deep water (90–500 m, Butler et al.[6]). Production process errors show a high level of autocorrelation (ρ=0.83–0.94, Table 3). Means, variances and autocorrelations for r_y were not very sensitive to assumptions about K (Table 3). There was no clear relationship between surplus production and biomass, but P_y was lowest at the highest and lowest B_y levels and autocorrelation in production process errors was obvious (Fig. 3A). The distribution of r_y values (Fig. 3B) was skewed to the right and there were no negative values. Gamma distributions fitted by maximum likelihood and the method of moments (Appendix 1) were similar in shape (Fig. 3).

Table 3

Summary statistics and gamma distribution parameters for annual process errors in the intrinsic population growth rate (r_y) for cowcod rockfish (*Sebastes levis*), estimated from stock assessment results (Butler et al.[6]). Parameters α and β, were estimated with fixed $\gamma = -M$ by maximum likelihood. K is the carrying capacity in the logistic population dynamics model. According to Butler et al.,[6] K=3400 metric tons (t) (95% confidence interval 2800–4000 t).

Parameter	K=84,500 t	K=99,400 t	K=103,000 t
Number B_y values ≤95% K	31	47	47
Sample mean	0.037	0.039	0.027
Sample variance	0.00059	0.00050	0.00021
Autocorrelation ρ	0.83	0.94	0.89
α	–0.055	–0.055	–0.055
β	17.7	19.0	36.1
$\gamma = -M$	0.0052	0.0049	0.0023
Mean	0.037	0.039	0.027
Variance	0.00048	0.00047	0.00019
Mode	0.032	0.034	0.025

With K=3400 t (Table 3), $\bar{r} = 0.039$ which suggests F_{MSY}= 0.0185/yr. This crude estimate is less than implied by the simple calculation $r = 2F_{MSY} = 0.11$ based on the proxy $F_{MSY} = M = 0.055$/yr, possibly because the natural mortality rate overestimates F_{MSY} for cowcod (Deriso, 1982). ASPIC estimates were similar ($F_{MSY} = 0.018$/yr with an 80% bootstrap confidence interval 0.00082–0.039/yr) to estimates based on $\bar{r}_y$. In simulations for cowcod, we used $\hat{F}_{MSY}$=0.018 (from ASPIC), $\sigma^2_{\bar{r}_y} = 0.00050$ and ρ=0.9.

Simulation model runs indicated that cowcod are very unlikely to rebuild to B_{MSY} in ten years. The mean generation time for cowcod is about 35 years (calculated as described by Restrepo et al., 1998). Simulations indicate that the mean time for rebuilding the stock with zero F is approximately 40 years (30–50 years, depending on model type). In accord with National Standard 1 Guidelines, it may be reasonable to develop plans with the goal of rebuilding the cowcod stock in 75 years or less. We therefore calculated and plotted 75-year, rather than 10-year rebuilding time isopleths, for cowcod rockfish.

Sensitivity analyses

We conducted three sensitivity analyses for each stock to determine if the choice of statistical distribution for stochastic $r_{s,y}$ values influenced rebuilding times in simulations. Sensitivity analyses used uncorrelated process errors and no uncertainty in F_{MSY} (model type 3). The first sensitivity analysis run for each stock was a nonparametric bootstrap (Efron, 1982) with $r_{s,y}$ values drawn randomly with replacement from the observed values (Eq. 6). The second and third sensitivity analyses run for each stock were parametric bootstraps with $r_{s,y}$ values drawn from a normal or lognormal distribution with the same mean (μ) and variance (σ^2) as the observed values (Tables 2–3, Figs. 2–3). To avoid bias in runs with the lognormal distribution (Beauchamp and Olson, 1973), log-transformed $r_{s,y}$ values were drawn from a normal distribution with mean $\ln(\mu) - \tau^2/2$ and variance $\tau^2 = \ln(CV^2+1)$, with CV= σ/μ (Jacobson et al., 1994). For convenience in programming, $r_{s,y}$ values in normal and lognormal runs were sampled with replacement from a fixed pool of 200 random numbers drawn from the proper statistical distribution at the outset of the simulation.

Results

Mean rebuilding times were longer than median rebuilding times in stochastic simulations (run types 2–6) for yellowtail flounder and cowcod rockfish because distributions of recovery times were skewed to the right (Figs. 4–5). Skewness (and the extent to which mean recovery times exceeded median recovery times) was more pronounced at lower starting biomass levels, at higher F levels, where there was more uncertainty about F_{MSY} and autocorrelation in process errors.

Skewed distributions for rebuilding times affected the shape of rebuilding time isopleths (Figs. 6–7). For all stochastic models of yellowtail flounder and most stochastic models of cowcod rockfish, isopleths for mean and median rebuilding times were widely separated. In addition, isopleths were asymmetrical. For example, the distance between median and $Q_{90\%}$ isopleths was greater than the distance between $Q_{10\%}$ and median isopleths. Separation of isopleths and asymmetry were greatest for model type 6 which had correlated process errors and uncertainty about F_{MSY}.

In simulations for both stocks, uncertainty about F_{MSY} had a greater effect than process error on the shape and separation between isopleths for $Q_{10\%}$, median, mean, and $Q_{90\%}$ rebuilding times. For example, in both stocks, there

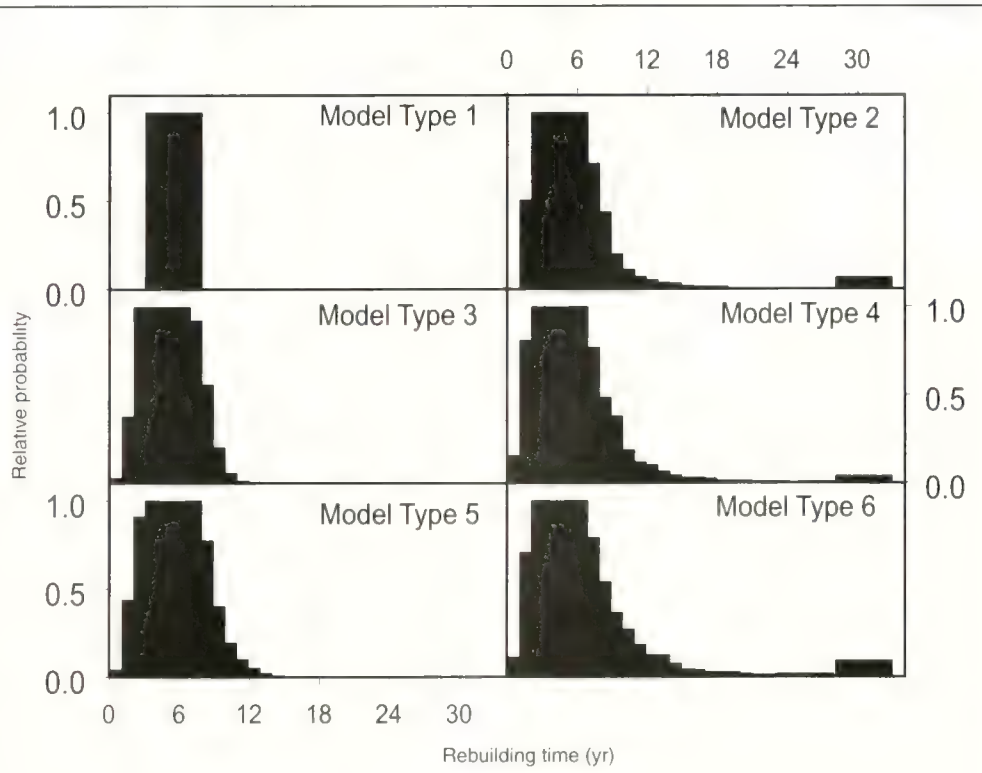

Figure 4

Distribution of simulated recovery times for Georges Bank yellowtail flounder from six types of logistic population growth models (type 1 deterministic, others stochastic, see Table 1) with F_{MSY}=0.30/yr, CV for uncertainty in F_{MSY}= zero or 20%, variance for production process errors zero or 0.037, and autocorrelation in process errors ρ=zero or 0.33. Results are for 2000 model runs starting from an initial biomass of B/B_{MSY} =0.19 and constant F=0.18/yr.

was more asymmetry and separation between isopleths (Figs. 6–7) for model type 2 (no process errors and with uncertainty about F_{MSY}) than for model type 3 (uncorrelated process error with no uncertainty about F_{MSY}).

The fishing mortality rate that gave a median recovery time of ten years for yellowtail flounder (or 75 years for cowcod rockfish) was generally higher than the fishing mortality rate that gave a corresponding mean recovery time from the same initial biomass level (Figs. 8–9). Similarly, the F that gave a mean recovery time of ten or 75 years was generally higher than the F that gave the corresponding $Q_{90\%}$ recovery time. There were some exceptions for cowcod at high F and initial biomass levels in runs with uncertainty in F_{MSY} (run types 2, 4, and 6) due to a few runs with very long rebuilding times. The very long rebuilding times in runs for cowcod with uncertainty were due to F in excess of the simulated true F_{MSY}.

Isopleth shape may be important in interpreting simulation results. For example, isopleths for 10-year median rebuilding times in all models for yellowtail flounder were steep for F in the range 0–0.2/yr (Figs. 8–9). Therefore, according to example model results, the probability of recovery in ten years is at least 50% for Georges Bank yellowtail flounder at biomass values ≥0.05 K, as long as fishing morality rates are less than 0.2/yr.

Seventy-five year stock-rebuilding time isopleths for cowcod rockfish were sensitive to assumptions about the distribution of production process errors but 10-year isopleths for yellowtail flounder were not (Figs. 10–11). We hypothesize that differences among statistical distributions r_y assumed in simulations were magnified for cowcod by long (e.g. 75 yr) rebuilding times (see "Discussion" section).

Rebuilding isopleths for cowcod based on r_y values from a gamma distribution had higher F, at a given biomass, than rebuilding isopleths based on the distribution of observed r_y values (Fig. 11). In other words, results based on the gamma distribution suggest a more productive cowcod stock, presumably because the distribution of r_y values for cowcod had more mass than the gamma distribution over low r_y values (<0.03/yr, Fig. 3).

Discussion

Managers should consider using median rebuilding time goals, in addition to mean or other quantiles, in develop-

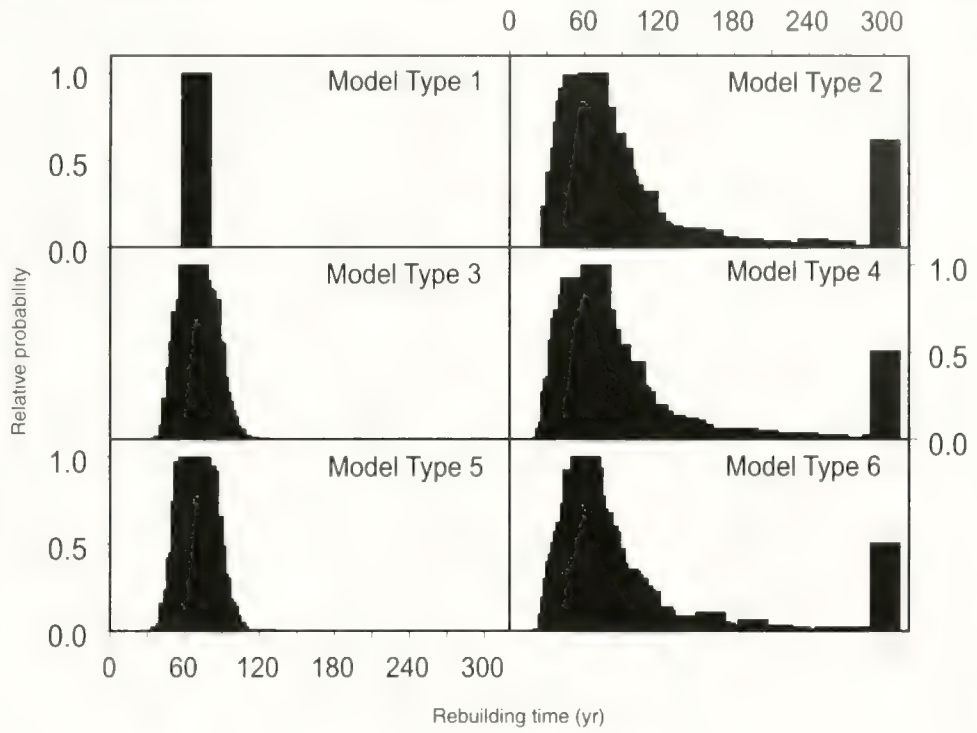

Figure 5

Distribution of simulated recovery times for cowcod rockfish in the Southern California Bight from six types of logistic population growth models (type-1 deterministic, others stochastic, see Table 1) with F_{MSY}=0.0.018 /yr, CV for uncertainty in F_{MSY}= zero or 20%, variance for production process errors zero or 0.037, and autocorrelation in process errors ρ=zero or 0.9. Results are for 2000 model runs starting from an initial biomass of B/B_{MSY} =0.19 and constant F=0.011/yr.

ing and evaluating rebuilding plans. This recommendation is based on a narrow technical consideration, i.e. that median recovery time calculations are less sensitive to model assumptions. A median rebuilding time plan is risk neutral in the sense that the probability of rebuilding times less than intended is the same as the probability of rebuilding times longer than intended (i.e. both 50%). Of course, rebuilding plans based on median rebuilding time goals will be more liberal in terms of short-term catch (i.e. have higher F) and have longer rebuilding times on average than plans based on mean or, for example, $Q_{90\%}$ rebuilding time goals. In summary, a manager who is willing to accept a 50% chance of rebuilding times greater that desired and who is concerned about model uncertainties, might choose a median rebuilding time approach.

A potential advantage in using percentiles other than the median is that managers can specify risk levels in trying to rebuild stocks. For example, managers could choose and evaluate rebuilding plans based on a $Q_{90\%}$ isopleth to insure at least a 90% chance of rebuilding in specified time period. However, $Q_{90\%}$ isopleths may be sensitive to model assumptions.

Approaches to using rebuilding time isopleths without relying on uncertain estimates of rebuilding time distributions (e.g. mean or $Q_{90\%}$), are an important area for future research. Cadrin (1999) used deterministic rebuilding time isopleths with the tenth percentile of the estimate for r. Isopleths for median rebuilding time might be used with lower bounds on confidence intervals for B_0 and B_0/K or upper bounds on current F, F_{MSY}, or F/F_{MSY}. Estimates of uncertainty in these parameters are often available (Prager, 1994) and can be incorporated in an *ad hoc* fashion. For example Butler et al.[6] suggest that B_{1998}/K for cowcod rockfish is 7% (CV about 30%) and that the F in 1998 was 0.085/yr (CV 34%). A risk-averse manager might implement a rebuilding plan that reduces that $F_{Threshold}$ to a point on the 75-year rebuilding time isopleth that lies above the lower boundary of a 95% confidence interval for biomass. Similarly, a risk-averse manager might select a rebuilding plan that reduces $F_{Threshold}$ to account for the upper bound on uncertainty in estimating F.

Uncertainty in F_{MSY} is an important factor to consider in rebuilding plans as F increases from low levels towards F_{MSY}. Expected rebuilding times increase at high F because F may exceed true F_{MSY} (assumed known but with

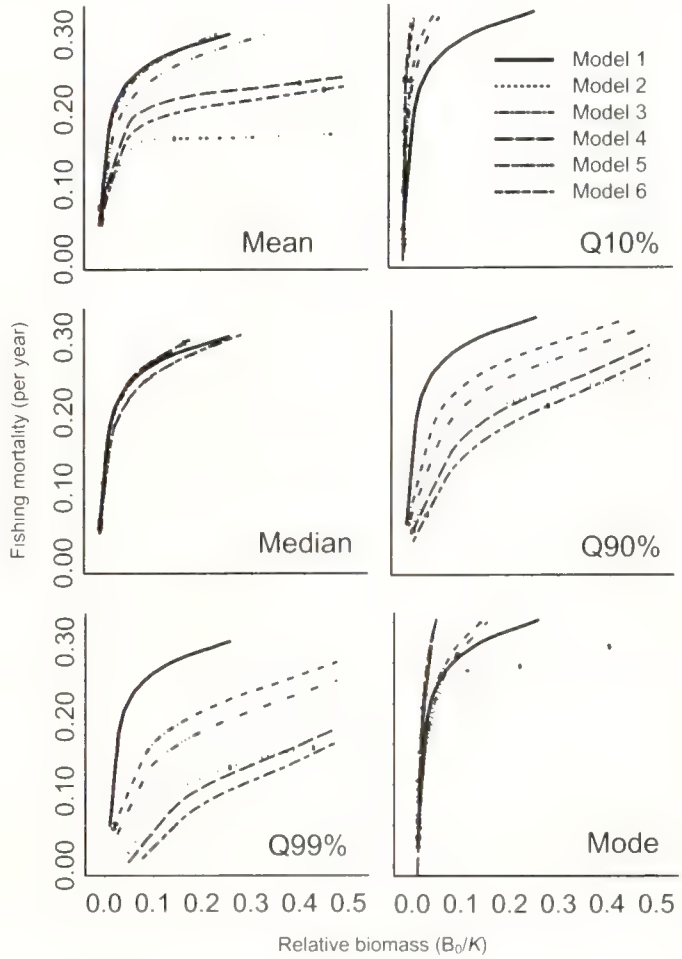

Figure 6

Isopleths for mean, median, mode, $Q_{10\%}$, $Q_{90\%}$, and $Q_{99\%}$ ten-year stock-rebuilding times simulated with six model types (Table 1) for Georges Bank yellowtail flounder. Isopleths for all statistics and one type of model are shown in each panel. Model types 2, 4, and 6 include uncertainty in F_{MSY}.

error) in a high proportion of cases (Figs. 8–9). Fortunately, process errors and autocorrelation may reduce this problem because stock growth rates increase in some years so that the true F_{MSY} exceeds the manager's estimate.

Stock-rebuilding times calculated with deterministic models approximate median rebuilding times from stochastic models. For example, rebuilding times in Cadrin (1999) calculated with a deterministic model for Georges Bank yellowtail flounder are very close to median rebuilding times from our stochastic models. From our results, we hypothesize that rebuilding time isopleths for other species (Applegate et al.[3]) based on Cadrin's (1999) deterministic model should also be viewed as approximations to isopleths for median rebuilding times.

Our simulation analyses indicate that rebuilding times for overfished stocks (with a range of life history characteristics, initial biomass levels and fishing mortality rates) tend to be skewed and can be highly variable (Figs. 4–5). Hence, rebuilding in any specific case may be quicker or take much longer than expected, particularly if expectations are based on deterministic models that approximate median rebuilding times. For example, probabilities of rebuilding times twice as long as the goal for Georges Bank yellowtail flounder (10 yr) and cowcod (75 yr) were 4% and 8% and probabilities of rebuilding times half as long were 40% and 1%.

Modeling choices

Stochastic models are necessary when estimates of mean rebuilding times or quantiles other than the deterministic approximation to the median are needed. Rebuilding time

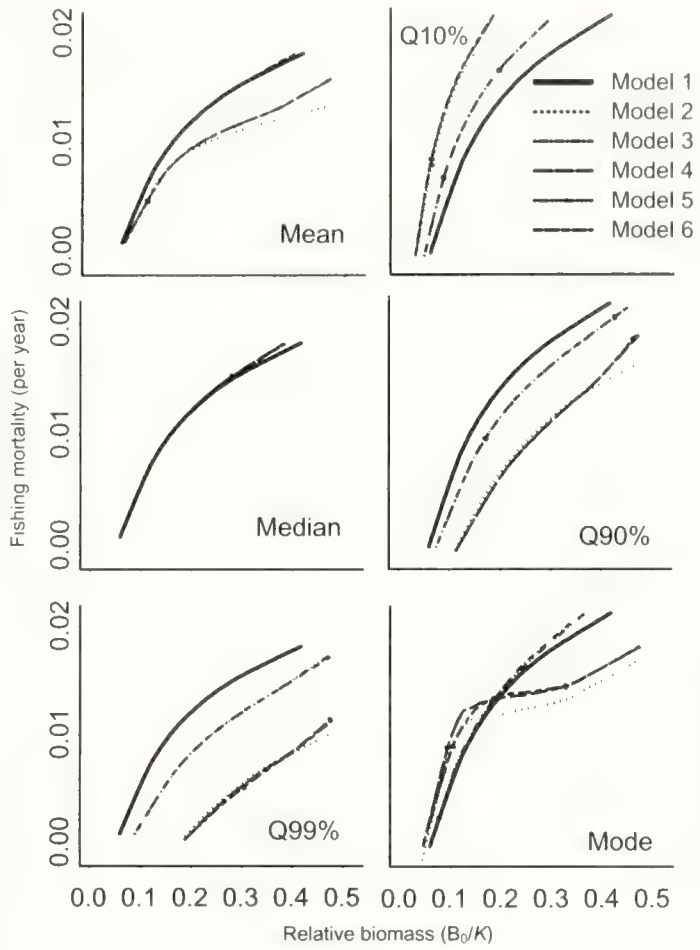

Figure 7

Isopleths for mean, median, mode, $Q_{10\%}$, $Q_{90\%}$, and $Q_{99\%}$ 75-year stock-rebuilding times simulated with six model types (Table 1) for cowcod rockfish in the Southern California Bight. Isopleths for all statistics and one type of model are shown in each panel. Model types 2, 4, and 6 include uncertainty in F_{MSY}

isopleths from deterministic model type 1 were quite different from isopleths (other than for median rebuilding times) from stochastic models.

Rebuilding time isopleths can be used with any type of population dynamics model. We used the logistic population growth model in this paper because it is clearly linked to B_{MSY} and F_{MSY}, incorporates density dependence, is easy to apply to a wide range of stocks (with varying amounts of information), and computationally efficient. However, rebuilding time isopleths could have been calculated by using Cadrin's[5] age-structured model for Georges Bank yellowtail flounder or Butler et al.'s[6] biomass dynamic model for cowcod rockfish. Age-structured models might be best for calculating rebuilding time isopleths if the rebuilding time frame is relatively short and estimates of abundance are available for several incoming year classes because age-structured models account for transient conditions (e.g. recruitment and growth patterns) that are important in the short term.

Age-based projections were used to test the expected performance of rebuilding targets for six New England groundfish stocks (NDWG[8]). The original rebuilding targets were derived from five-year rebuilding time isopleths calculated with a deterministic logistic growth models, but the targets incorporated estimation uncertainty by assuming the tenth percentile of the estimate

[8] NDWG (Northern Demersal Working Group). 2000. Assessment of 11 northeast groundfish stocks through 1999. Northeast Fisheries Science Center Reference Document 00-05, 175 p. Northeast Fisheries Science Center, 166 Water Street, Woods Hole, MA, 02543.

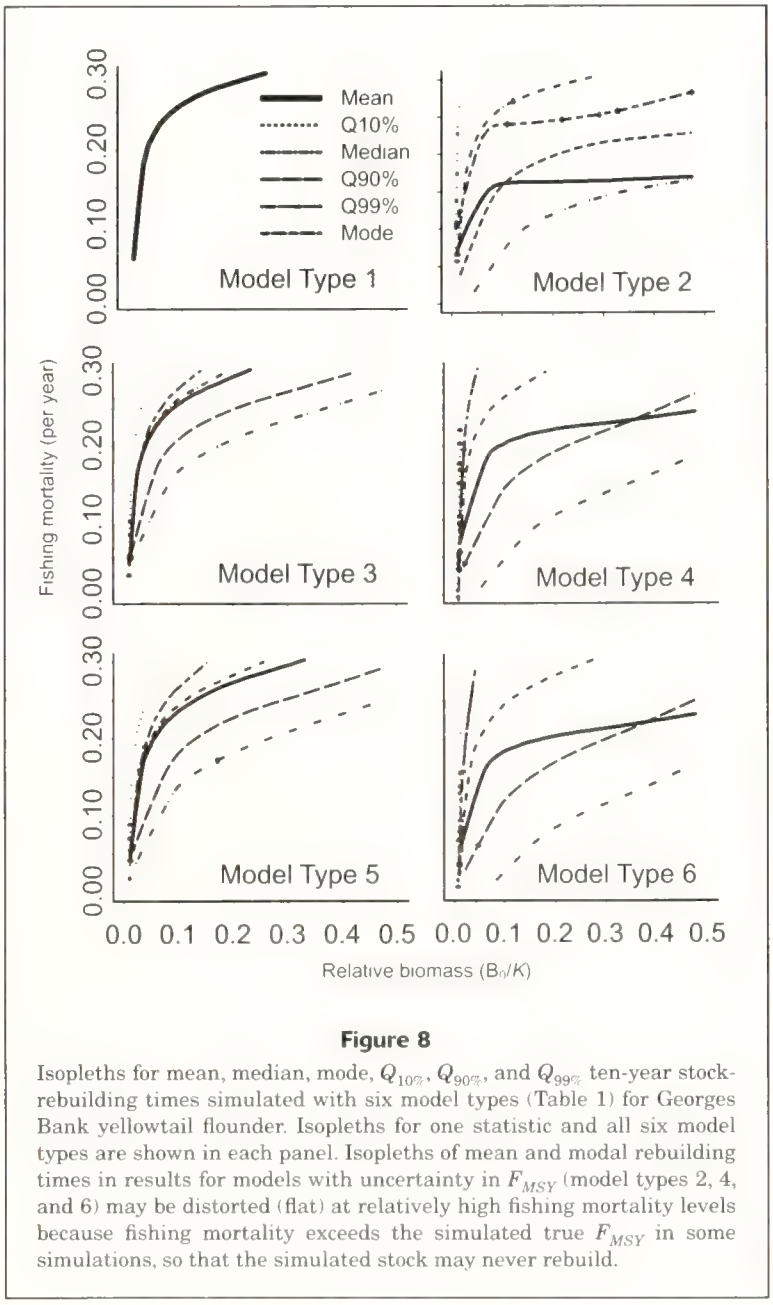

Figure 8

Isopleths for mean, median, mode, $Q_{10\%}$, $Q_{90\%}$, and $Q_{99\%}$ ten-year stock-rebuilding times simulated with six model types (Table 1) for Georges Bank yellowtail flounder. Isopleths for one statistic and all six model types are shown in each panel. Isopleths of mean and modal rebuilding times in results for models with uncertainty in F_{MSY} (model types 2, 4, and 6) may be distorted (flat) at relatively high fishing mortality levels because fishing mortality exceeds the simulated true F_{MSY} in some simulations, so that the simulated stock may never rebuild.

of r (Cadrin, 1999; Applegate et al.[3]). For the six stocks, starting biomass in 1999 ranged from 25% to 93% of B_{MSY} and estimates of F_{MSY} ranged from 0.5 to 0.8. Estimated rebuilding times averaged 3.5 years (ranging from 1 to 7 yr) for 50% probability of attaining B_{MSY} (NDWG[8]). Therefore, the age-based simulations indicated that isopleths based on deterministic biomass dynamic models generally performed well for overfished New England groundfish stocks. Brodziak et al. (2001) analyzed stock-recruit data and concluded that "(1) time horizons for rebuilding will be uncertain, owing to recruitment variability, (2) some productive stocks (haddock, yellowtail flounder) have serial correlation in recruitment and this may either enhance or diminish chances for stock recovery." Thus, results with surplus production models, age-structured models, and stock-recruit analyses highlight the fundamental similarities between a wide range of modeling approaches (Sissenwine and Shepherd, 1987).

The best choice of stochastic simulation model for developing and evaluating rebuilding plans will depend on the situation. Sainsbury (1993) concluded that models incorporating simple assumptions about population dynamics were more appropriate for evaluating performance of control rules than models with more complex assumptions. PFMC[1] used a simple model incorporating environmental effects on recruitment with useful results. However, Bell

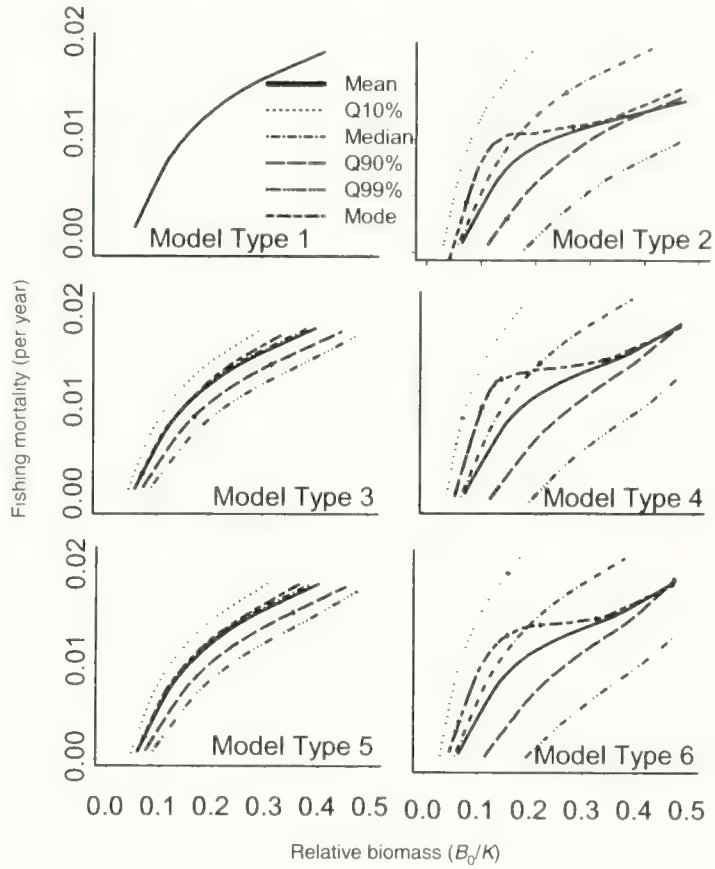

Figure 9

Isopleths for mean, median, mode, $Q_{10\%}$, $Q_{90\%}$, and $Q_{99\%}$ 75-year stock-rebuilding times simulated with six model types (Table 1) for cowcod rockfish in the Southern California Bight. Isopleths for one statistic and all six model types are shown in each panel. Model types 2, 4, and 6 include uncertainty in F_{MSY}. Isopleths of mean and modal rebuilding times in results for models with uncertainty in F_{MSY} (model types 2, 4, and 6) may be distorted (flat) at relatively high fishing mortality levels because fishing mortality exceeds the simulated true F_{MSY} in some simulations so that the simulated stock may never rebuild.

and Stefansson[9] and Patterson (1999) used more complex simulation models with success.

Distributional assumptions

Simulation analyses (Figs. 10–11) indicate that the choice of statistical distribution for simulating process errors in model parameters (e.g. r_y) may be important, particularly when rebuilding times are long (e.g. those for cowcod rockfish) due to low stock productivity, low stock biomass, unproductive stock dynamics, or autocorrelation in process errors. The choice of statistical distributions for simulating r_y involves choosing between theoretical distributions supported by theory (e.g. autocorrelated gamma distribution with negative values bounded below at $-M$) or bootstrap distributions of observed values. The programming and work required to experiment with alternative distributions is not overwhelming and we recommend sensitivity analyses in cases where distributional assumptions may be important.

Theoretical distributions for stochastic parameters are flexible because many types of distributions are available, most can be modified to include autocorrelation, most can

[9] Bell, E. D., and G. Stefansson. 1998. Performance of some harvest control rules. NAFO (North Atlantic Fisheries Organization) SCR Doc. 98/7, 1–19. Northwest Atlantic Fisheries Organization, 2 Morris Drive, P. O. Box 638, Dartmouth, Nova Scotia, B2Y 3Y9, Canada.

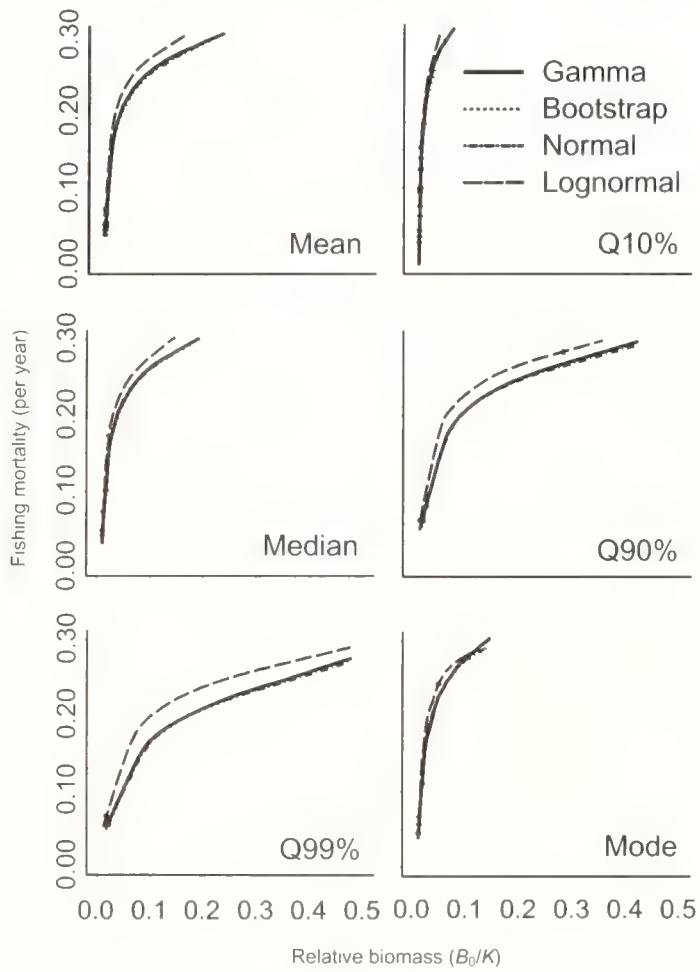

Figure 10

Mean, median, mode, $Q_{10\%}$, $Q_{90\%}$, and $Q_{99\%}$ ten year stock-rebuilding time isopleths for Georges Bank yellowtail flounder, simulated with model type 3 (no uncertainty about F_{MSY} and uncorrelated r_y values). Stochastic r_y values were from a gamma distribution (same as Figs. 6 and 8), normal distribution, lognormal distribution, or bootstrap of observed r_y values. All distributions had the same mean and variance.

be modified to include negative or extreme values not evident in short observed time series, and most can give the same mean, variance and autocorrelation levels as estimated from available data. However, as in the case of Georges Bank yellowtail flounder and cowcod, the shape of theoretical and observed distributions may not match closely (Figs. 2–3).

In comparing theoretical and observed distributions for model parameters (e.g. Figs. 2–3), it is important to remember that most observed distributions are based on relatively few observations (Table 2). Furthermore, observed values may be autocorrelated (ρ=0.33 for Georges Bank yellowtail flounder and ρ=0.94 for cowcod rockfish, Tables 2–3). High levels of autocorrelation reduce the "effective" number of observations dramatically so that observed values may provide a poor estimate of the shape of their distribution (Bartlett, 1946; Bayley and Hammersley, 1946). For example, Equation 16 in Bayley and Hammersley, with estimated autocorrelations (lags of 1–13 years) for Georges Bank yellowtail flounder, gives an effective sample size n^*=17 (compared to n=25 r_y values). For cowcod rockfish (with autocorrelations for lags 1–17), n^*=11 (compared to n=47 r_y values). Thus, autocorrelation in r_y values may reduce the effective sample size and information used to estimated the shape, mean and variance of statistical distributions for r_y values by about 32% for Georges Bank yellowtail flounder and 77% for cowcod rockfish.

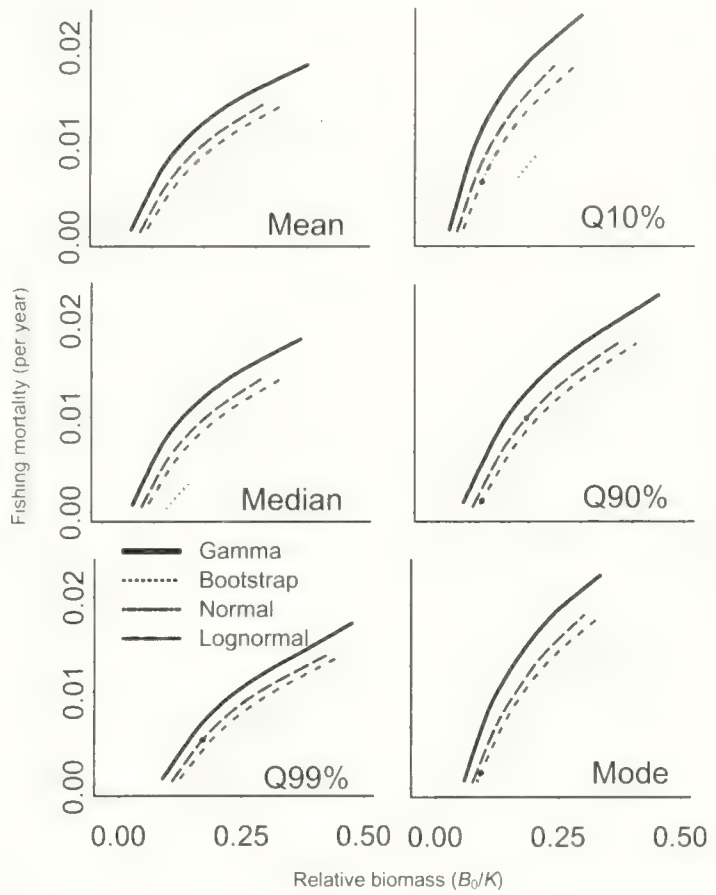

Figure 11

Mean, median, mode, $Q_{10\%}$, $Q_{90\%}$, and $Q_{99\%}$ 75-year stock-rebuilding time isopleths for cowcod rockfish, simulated with model type 3 (no uncertainty about F_{MSY} and uncorrelated r_y values). Stochastic r_y values were from a gamma distribution (same as Figs. 7 and 9), normal distribution, lognormal distribution or bootstrap of observed r_y values. All distributions had the same mean and variance.

Developing, monitoring, and evaluating stock-rebuilding programs

Once the management goal, desired probability of achieving the stock-rebuilding goal, and the time frame for rebuilding are identified (e.g.10-yr median rebuilding time to a B_{MSY} target), the simplest way to use stock-rebuilding time isopleths in designing a rebuilding plan is to choose a constant-F_{B_0} level from the appropriate rebuilding time isopleth, based on a current estimate of B_0. Cadrin (1999) has provided an example of this approach.

Stock-rebuilding time isopleths can be used to monitor the progress of any rebuilding plan although interpretation is clearest with constant-F values (Cadrin, 1999). For example, the point defined by current biomass and F for Georges Bank yellowtail flounder in the second year (1997) of a hypothetical five-year rebuilding plan beginning in 1996 should lie near or within the 3-year rebuilding time isopleth (Fig. 1). If the point lies far outside the 3-year isopleth, then managers could be sure that the rebuilding plan was behind schedule.

Evaluating harvest control rules as stock-rebuilding programs

It may be necessary to evaluate harvest control rules that allow F to vary with biomass (e.g. the common harvest control rule in Fig. 1) as a rebuilding plan. Rebuilding isopleths provide guidance in this situation because they can be used to reject some harvest control rules based on a single necessary criterion. However, the test is weak because a harvest control rule that passes the test may or

may not be sufficient as a rebuilding plan. In this context, it is important to remember that rebuilding time isopleths are constructed based on the assumption of constant fishing mortality rates during the rebuilding program. More complicated rebuilding plans, that allow F to vary according to changes in biomass or other factors, are best evaluated by stock-specific simulations.

The test is based on the notion that control rules that allow F levels above the stock-rebuilding time isopleth for biomass levels above B_0 are unlikely to rebuild the stock with desired probability in the desired time frame. Therefore, as a minimum requirement for meeting rebuilding time goals, harvest control rules used as rebuilding plans should lie on or under the corresponding rebuilding time isopleth for all biomass levels above B_0. Consider a hypothetical overfished stock for which there is a ten-year median rebuilding time goal. Assume that a harvest control rule proposed as a rebuilding plan has the typical shape (i.e. F increases or stays the same as biomass increases, as in Fig. 1). If the control rule lies above the isopleth for some critical biomass level between B_0 and B_{MSY}, then the rule will allow fishing mortality rates that are generally too high to meet management goals once biomass reaches the critical level.

The example of Georges Bank yellowtail flounder

Georges Bank yellowtail flounder (Fig. 1) can be used to illustrate how rebuilding time isopleths might have been used to evaluate stock-rebuilding plans for hypothetical implementation during 1996 and how stock-rebuilding time isopleths can be used to monitor progress in rebuilding overfished stocks. The discussion is hypothetical, however, because the examples evaluate management approaches that have not been used in rebuilding the stock. In reality, managers kept F for Georges Bank yellowtail flounder during 1996–99 nearly constant at a level well the below the 10-year isopleth, and the Georges Bank yellowtail flounder stock was almost rebuilt to the B_{MSY} target level in 1999 after only four years (Fig. 1).

Based on this example, the harvest control rule in Figure 1 would have been marginal for use in a hypothetical median ten-year stock-rebuilding plan for Georges Bank yellowtail flounder starting in 1996, because the rule lies slightly above the 10-year isopleth for biomass levels of 47% B_{MSY}. The harvest rule might have been rejected outright as a five-year rebuilding plan because the rule lies well above the 5-year rebuilding time isopleth. The rebuilding trajectory for Georges Bank yellowtail flounder (Fig. 1) shows that the five-year rebuilding plan, which began in 1996, was on schedule during 1996–98 because fishing mortality and estimated biomass were within the 5-year, 4-year, and 3-year isopleths during successive years.

The Georges Bank yellowtail flounder example provides an important final lesson about uncertainty in actual rebuilding times, even if statistical distributions of potential rebuilding times are characterized accurately. During 1996–99, the stock was managed at a relatively constant F level that was well above the entire 4-year median rebuilding time isopleth (Fig. 1). Despite the relatively high F level, Georges Bank yellowtail flounder reached a biomass level near B_{MSY} in 1999, after four years. We attribute this fortunate chain of events to stochastic variation in process errors stemming primarily from recruitment and growth of the strong 1997 year class (Cadrin[5]).

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Appendix 1—Independent process errors

We simulated independent production process errors using a three-parameter gamma probability distribution (Johnson et al., 1994). The gamma probability density function for independent (no autocorrelation) r_y values in one simulation (denoted as s) was

$$P(r_{y,s} \mid \alpha_s, \beta_s, \gamma) = \frac{(r_{y,s} - \gamma)^{\alpha_s - 1} e^{-(r_{y,s} - \gamma)/\beta_s}}{\beta_s^{\alpha_s}\,\Gamma(\alpha_s)}, \qquad (1)$$

where $\Gamma(\alpha_s)$ is the gamma function and the parameters of the gamma distribution are $\alpha_s > 0$, $\beta_s > 0$ and γ.

The expected (mean) value for r_y values from the three-parameter gamma distribution is $\beta_s \alpha_s + \gamma$ and the variance is $\beta_s^2 \alpha_s$. The parameter γ defines a minimum value for the distribution of r_y values; therefore we set $\gamma = -M$ (see text). There were too little data to directly estimate the lower-bound γ for either of the species in our analysis because years with negative production occurred infrequently for stocks in our analysis. The three-parameter gamma distribution has a single mode at $\gamma + \beta_s(\alpha_s - 1)$ if $\alpha_s > 1$. When $\alpha_s \leq 1$, the probability distribution function declines monotonically as r_y increses from the minimum value at $r_y = \gamma$.

The mode for empirical r_y values in our study was always larger than $-M$ so that α_s was larger than one.

Maximum likelihood estimates of the parameters α and β for each stock (conditional on the assumption $\gamma=-M$) were obtained iteratively in a spreadsheet by maximum likelihood with observed r_y values as data. In simulations, we used the simpler method of moments to calculate gamma distribution parameters. Given $\gamma=-M$ and estimates of the mean (μ) and variance (σ^2) for r_y values from real data, the method of moments solves the two equations $\mu=(B\alpha+\gamma)$ and $\sigma^2=\alpha\beta^2$ for the two unknowns α and β. In particular $\beta=\sigma^2/(\mu-\gamma)$ and $\alpha=\sigma^2/\beta^2$. The maximum likelihood approach and method of moments gave similar parameter estimates for real data sets (Figs. 2–3) suggesting that the method of moments was acceptable for simulations. In what comes later, maximum likelihood parameter estimates from data ($\hat{\alpha}$, $\hat{\beta}$, $\gamma=-M$) are distinguished from simulated values calculated by the method of moments ($\tilde{\alpha}_s$, $\tilde{\beta}_s$, $\gamma=-M$).

In each simulation run, the assumed "true" value of $F_{MSY,s}$ was used to calculate $\bar{r}_s = 2F_{MSY,s}$. In simulation runs with no process error the simple calculation $r_{s,y}=\bar{r}_s$ was used. In runs with process error, $\bar{r}_s$, was the mean of the distribution of stochastic $r_{s,y}$ values (see below).

For runs with independent process errors (no autocorrelation), annual logistic parameter values $r_{s,y}$ were drawn from a gamma distribution with parameters ($\tilde{\alpha}$, $\tilde{\beta}$, γ) calculated by the method of moments from the mean $\bar{r}_s$ and variance $\sigma^2_{r_y}$ estimated from empirical data.

Appendix 2—Autocorrelated process errors

This appendix describes two algorithms for generating autocorrelated production process errors from gamma distributions. The algorithms are based on first-order autoregressive and moving average error structures used in time-series analysis (Nelson, 1973). The shapes of original uncorrelated gamma distributions and new, correlated probability distributions for both algorithms appeared identical in plots.

Algorithm 1 was for autocorrelations (ρ) in the range zero to 0.5:

$$r_{s,y} = d_{s,y} + \theta d_{s,y-1}, \tag{1}$$

where $r_{s,y}$ = was the logistic population growth parameter for year y in simulation run s, and the moving average parameter (θ) was

$$\theta = -1+\sqrt{\frac{1-4\rho^2}{2\rho}}, \tag{2}$$

with θ in the range (0,1). The random numbers $d_{s,y}$ in algorithm 1 were drawn from a gamma distribution with parameters:

$$\alpha_{s,y} = \tilde{\alpha}_{s,y}\frac{(1+\theta^2)}{(1+\theta)^2} \tag{3}$$

$$\beta_{s,y} = \tilde{\beta}_{s,y}\frac{(1+\theta)}{(1+\theta^2)} \tag{4}$$

and $\gamma=-M$. The adjusted parameter values ($\ddot{\alpha}_s$, $\ddot{\beta}_s$, γ) make the mean and variance of autocorrelated $r_{s,y}$ values from algorithm 1 the same as for an independent series drawn from a gamma distribution with parameters $\tilde{\alpha}_s$,$\tilde{\beta}_s$,γ (see Appendix 1).

Algorithm 2 was for autocorrelations (ρ) in the range (0.5, 1):

$$r_{s,y} = \frac{\sum_{j=1}^{L} d_{s,y-1+j}}{L}, \tag{5}$$

where the random numbers $d_{s,y}$ were drawn from gamma distributions with parameters $\ddot{\alpha}_{s,r} = \tilde{\alpha}_{s,r}/L$, L an integer >3, $\ddot{\beta}_{s,r} = \beta_{s,r}L$, and γ. The adjusted parameter values make the mean and variance of the autocorrelated and independent $r_{s,y}$ values the same.

The autocorrelation in algorithm 2 is $\rho=(L-1)/L$. For simulations, we chose the smallest value of L that gave an autocorrelation that was at least as large as the value desired. Extremely high autocorrelations (e.g. $\rho>0.9$) can give $\ddot{\alpha}_{s,y} = \tilde{\alpha}_{s,y}/L \leq 1$ when $\tilde{\alpha}_{s,r}$ is near L. This was a minor problem in some cases because gamma distributions for $d_{s,y}$, and autocorrelated values of $r_{s,y}$, have no mode when $\ddot{\alpha}_{s,y} \leq 1$. We avoided this, where necessary, by setting the maximum value of L to 10 (ρ=0.90) and constraining $\ddot{\alpha}_{s,y} \leq 1$ in simulations.

Nuclear and mitochondrial DNA markers for specific identification of istiophorid and xiphiid billfishes*

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Abstract—Independent molecular markers based on mitochondrial and nuclear DNA were developed to provide positive identification of istiophorid and xiphiid billfishes (marlins, spearfishes, sailfish, and swordfish). Both classes of markers were based on amplification of short segments (<1.7 kb) of DNA by the polymerase chain reaction and subsequent digestion with informative restriction endonucleases. Candidate markers were evaluated for their ability to discriminate among the different species and the level of intraspecific variation they exhibited. The selected markers require no more than two restriction digestions to allow unambiguous identification, although it was not possible to distinguish between white marlin and striped marlin with any of the genetic characters screened in our study. Individuals collected from throughout each species' range were surveyed with the selected markers demonstrating low levels of intraspecific character variation within species. The resulting keys provide two independent means for the forensic identification of fillets and for specific identification of early life history stages.

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Species-level identification of most marine fishes is typically based on adult characters. However, distinguishing characters may be removed from adults when they are processed for market or personal consumption, making such identification problematic. Furthermore, species identification from early life history stages of many marine fishes is not possible because diagnostic morphological characters at these stages are not currently known. Consequently, alternative means of identification are needed.

A variety of molecular genetic characters have been used to provide identifications of marine fishes. Marine fish eggs and larvae have been identified by using allozymes (Mork, et al., 1983; Graves et al., 1988), restriction analysis of whole mitochondrial (mt) DNA (Daniel and Graves, 1994), restriction analysis of specific mtDNA gene regions (Luczkovich et al.[1]), and specific amplification of mtDNA gene regions (Rocha-Olivares, 1998). A similar suite of molecular markers has been used to provide positive identification of adult marine fish tissues, with recent emphasis on restriction analysis of amplified regions of the mitochondrial genome (Chow et al., 1993; Chow 1994, Chow and Kishino, 1995; Heist and Gold, 1997; Innes et al., 1998; Cordes et al., 2001).

To be effective, a diagnostic molecular marker must demonstrate consistent differences among closely related species and exhibit very limited intraspecific variation. Restriction analyses of regions of the mitochondrial genome have met these criteria for several marine fishes. However, reliance on a single, maternally inherited character (mtDNA) can provide misleading results in situations where there is a possibility of hybridization or introgression, and analyses of both nuclear and mitochondrial markers are therefore desirable.

The istiophorid and xiphiid billfishes (marlins, spearfishes, sailfish and swordfish) represent an important commercial and recreational fisheries resource. Because of depleted stock levels, current regulations within the United States prohibit the sale of istiophorid billfish taken in the Atlantic Ocean. Although adult billfishes are easily identified on the basis of morphological characters, these characters are typically removed during processing, preventing morphological identification. In addition, the early life history stages of istiophorid billfishes are not well known, and specific identification is problematic (Nakamura, 1985).

Chow (1994) used 13 restriction enzymes in a restriction fragment length polymorphism (RFLP) analysis of a 350-bp region of the mtDNA cytochrome *b* gene to discriminate among ten nominal species of billfishes; however samples sizes were small for several species

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[1] Luczkovich, J.J., H.J. Daniel, M.W. Sprague, S. E. Johnson, R. C. Pullinger, T. Jenkins, and M. Hutchinson. 1999. Characterization of critical spawning habitats of weakfish, spotted seatrout and red drum in Pamlico Sound using hydrophone surveys. Final report to the North Carolina Division of Marine Fisheries under grant numbers F-62-1 and F-62-2, 128 p. North Carolina Department of Environment and Natural Resources, Division of Marine Fisheries. Morehead City, NC 28557.

and banding patterns differed by as little as 15 base pairs, making alternate patterns difficult to distinguish. Innes et al. (1998) were able to discriminate among seven species of billfish found in Australian waters with RFLP analysis of a 1400-bp region of the mtDNA control region (D-loop). Their analysis, which employed four restriction enzymes, revealed relatively high levels of intraspecific variation of the diagnostic characters within some species, and there was some overlap of banding patterns between species. In neither study was an independent nuclear marker developed to corroborate specific identifications based on analyses of mtDNA.

In this article we present a molecular key to the identification of istiophorid and xiphiid billfishes using RFLP analyses of independent mitochondrial and nuclear DNA regions. We demonstrate low intraspecific variation of the characters within large collections of individuals sampled from throughout each species' range and show the utility of the markers for the identification of fillets and early life history stages.

Materials and methods

Collections of striped marlin (*Tetrapturus audax*), white marlin (*Tetrapturus albidus*), blue marlin (*Makaira nigricans*), and sailfish (*Istiophorus platypterus*) were available from previous analyses of stock structure (Graves and McDowell 1994, 1995; Graves, 1998), and individuals from locations throughout each species' range were selected for the present study (Table 1). These DNA samples consisted of the nuclear and mitochondrial bands resulting from mtDNA purifications with the equilibrium density gradient centrifugation protocols of Lansman et al. (1981). Samples of black marlin (*Makaira indica*), longbill spearfish (*Tetrapturus pfluergeri*), shortbill spearfish (*Tetrapturus angustirostris*), and swordfish (*Xiphias gladius*), were obtained from recreational and commercial fishermen (Table 1) and consisted of either frozen heart tissue or white muscle tissue preserved in DMSO storage buffer (Seutin et al., 1991). DNA was extracted from these tissues following the protocols of Winnepenninckx et al. (1993).

Evaluation of candidate mitochondrial and nuclear loci involved a two-step process. The first was to ensure consistent amplification by the polymerase chain reaction (PCR) of a similar-size product across all taxa. The second step was to screen those loci that successfully amplified across all billfish species with a panel of restriction endonucleases to identify enzymes that discriminated among species and revealed limited intraspecific variation.

Several candidate mitochondrial and nuclear gene regions were amplified by PCR (Table 2). The 25 μL PCR reactions consisted of 0.25 μL template DNA, 2.5 μL 10X PCR buffer plus magnesium, 0.5 μL dNTP mix, 0.25 μL forward primer, 0.25 μL reverse primer, 0.125 μL *Taq* DNA polymerase, and 21.125 μL PCR grade water. Primers were ordered from either Life Technologies (Gaithersburg, MD) or Genosys Biotechnologies Inc. (The Woodlands, TX), and PCR reactions were carried out in an MJ Research Corporation PTC-200 Peltier thermal cycler (Watertown, MA) by using the Life Technologies PCR reagent system (Gaithersburg, MD). Initial screening demonstrated that the mitochondrial ND4 gene region and the nuclear MN32-2 locus produced the most reliable amplifications across taxa and PCR conditions were optimized for these loci. The cycling parameters for the ND4 gene region were an initial denaturation at 95°C for 5 min., followed by 35 cycles of 94°C for 1 min., 47°C for 1 min., 65°C for 3 min., and a final extension at 65°C for 7 min. Amplification of MN32-2 proceeded with an initial denaturation at 95°C for 5 min., 40 cycles of 94°C for 1 min., 57°C for 1 min., 65°C for 3 min., and a final extension at 72°C for 7 min. Amplified products were held at 4°C until use. The size of each amplification product was determined on a 1% agarose gel run in TBE (45 mM Tris, 45 mM boric acid, I mM EDTA) at 100 volts for 1 hour. ND4 amplification resulted in a product of approximately 1.7 kb and MN32-2 amplification resulted in a product of approximately 1.2 kb.

Amplified products were screened with a panel of restriction endonucleases to identify those that discriminated among species, and revealed a minimum level of variation within species. All enzymes were purchased from Gibco/BRL Life Technologies Inc. (Bethesda, MD) with the exception of *Ban*I, which was purchased from Promega (Madison, WI). All were used according to the manufacturers' instructions.

Restriction fragments were separated on 2.5% horizontal agarose gels made from 1.25% UltraPure agarose (Life Technologies Inc., Bethesda, MD) and 1.25% NuSeive

Table 1

Collection information for billfish samples surveyed.

Species	Location	Number	Total
Sailfish	Brazil	34	99
	Mexico	24	
	Ecuador	17	
	Australia	24	
White marlin	Brazil	38	99
	Morocco	36	
	Venezuela	25	
Striped marlin	Mexico	28	96
	Ecuador	38	
	Australia	30	
Black marlin	Ecuador	12	60
	Australia	48	
Spearfish	Venezuela	12	16
	Hawaii	4	
Blue marlin	Mexico	24	150
	Australia	4	
	Ecuador	20	
	Hawaii	63	
	Jamaica	39	
Swordfish	Hawaii	20	20

Table 2

Primer pairs used to amplify regions evaluated in this study.

Locus	Primer sequence (5′–3′)	Source
Cytochrome b:		
CYTB-F	TGGGSNCARATGTCNTWYTG	Joseph Quattro, personal commun.[1]
CYTB-R	GCRAANAGRAARTACCAYTC	
ATPase 6:		
ATPase L8331	TAAGCRNYAGCCTTTTAAG	Joseph Quattro, personal commun.[1]
ATPase H8969	GGGGNCGRATRAANAGRCT	
D-Loop:		
CB3R-L	CATATTAAACCCGAATGATATTT	Palumbi et al., 1991
12SAR-H	ATAGTGGGGTATCTAATCCCAGTT	
ND4:		
ND4 ARG-BL	CAAGACCCTTGATTTCGGCTCA	Bielawski and Gold, 1996
ND4 LEU	CCAGAGTTTCAGGCTCCTAAGACCA	
ITS:		
ITS-3	TATGCTTAAATTCAGCGGGT	Goggin, C.L, 1994
ITS-5	CGTAGGTGAACCTGCGGAAGG	
SACTIN:		
SACSMSF-F	CGGACGCCCCCGTCACCAGGTAC	This study
SACIN-R	CCAGAGGCATACAGGGACAGCACAGC	
MN32-2:		
MN32-2F	GTAGCAAGGGGCTGTTGCATAG	Buonaccorsi et al., 1999
MN32-2R	GAGTCAGTGGTTCGGGATTTTATC	
MN47:		
MN47-F	GCTGTTGACCCAAACAATCCGG	Buonaccorsi et al., 1999
MN47-R	GGGCATAAATGCTCAGGACACTT	
MN81:		
MN81-F	CACTCAAACAGGTGAATCCTGGC	Buonaccorsi et al., 1999
MN81-R	CAAAACAACAGATGCCGCTAAGG	
WM08:		
WM08F	AGCAGCTAGGGACACACGATTCC	Buonaccorsi et al., 1999
WM08R	GGCAAACCTTACACTGAGGGGATG	

[1] Quattrro, J. 1995. Personal commun. Department of Biological Sciences, University of South Carolina College of Science and Mathematics, Columbia, SC, 29208.

GTG agarose (FMC BioProducts, Rockland, ME), and visualized under UV light after having been stained with ethidium bromide. Fragment sizes were estimated by comparison with a 1-kb size standard (Life Technologies Inc., Bethesda, MD) using RFLPScan Plus 3.0 (Scanalytics, Billerica, MA).

Results

Mitochondrial marker

Four mtDNA regions (cytochrome *b*, D-loop, ND4, and ATPase) were included in the initial screening (Table 2). The ATPase region was tested with eight potentially useful enzymes based on published sequences and was found to have an extremely low level of interspecific variation (many species exhibiting identical banding patterns). The cytochrome *b* region was screened with four enzymes based on published sequences, but because of the small size of the amplification product (350bp), differences in banding patterns were small and difficult to distinguish. The D-loop region was screened with a total of 40 enzymes. Of these, *Bcl* I, *Alu* I, *Rsa* I, and *Hinf* I were tested with up to 50 individuals from each species. Banding patterns that were initially thought to be diagnostic for blue marlin based on *Rsa* I were found to occur at low frequency in sailfish. This overlap combined with the large amount of intraspecific variation in some species made this region unsuitable for use as a forensic marker. Finally, the ND4 region was screened with a total of 47 restriction enzymes. Of these, 17 were tested more extensively, and the combi-

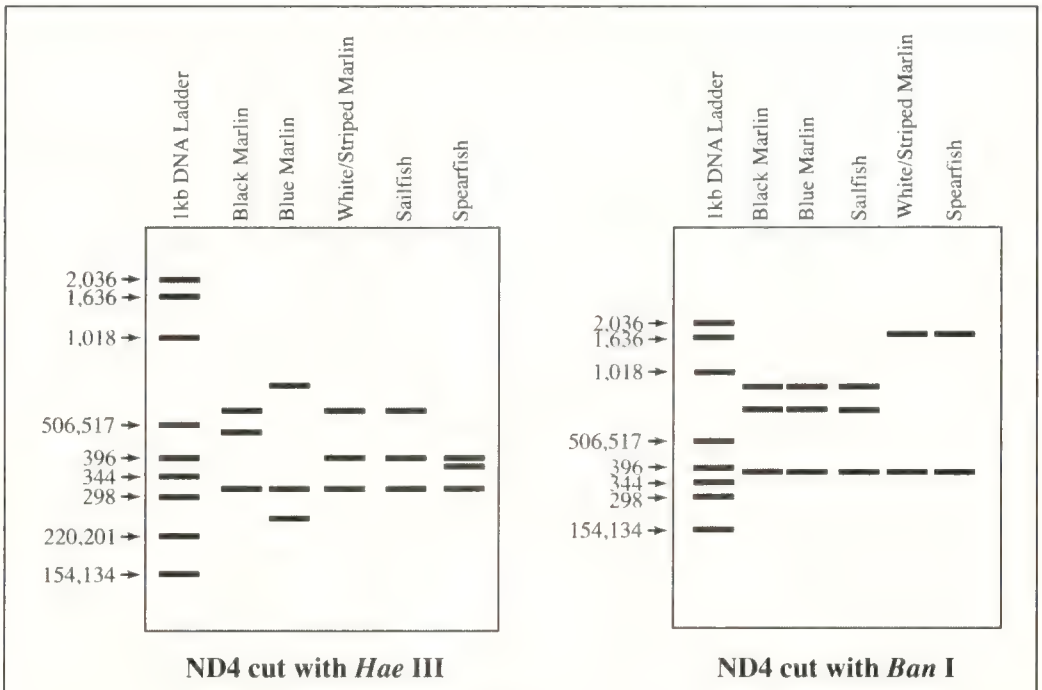

Figure 1

ND4 gel. Most common restriction fragment patterns of the ND4 mitochondrial gene region of istiophorid billfishes. (**A**) Digestion with *Hae* III. From left to right, 1-kb DNA ladder, black marlin (pattern D), blue marlin (pattern A), white and striped marlin (pattern B), sailfish (pattern B), shortbill spearfish (pattern E), and longbill spearfish (pattern E). (**B**) Digestion with *Ban* I. From left to right, 1-kb DNA ladder, black marlin (pattern A), blue marlin (pattern A), white and striped marlin (pattern B), sailfish (pattern A), shortbill spearfish (pattern B), and longbill spearfish (pattern B).

Table 3

Restriction fragment patterns of the mitochondrial ND4 region of istiophorid and xiphiid billfishes. Only diagnostic bands are shown.

(**A**) Digestions with *Hae* III. A = blue marlin; B = striped marlin, white marlin, sailfish; C = white marlin, sailfish; D = black marlin; E = spearfish; F = white marlin; G = spearfish; H = swordfish.

A	B	C	D	E	F	G	H
800	570	800	570	405	570	405	950
320	405	405	530	380	405	320	300
270	320	320	320	320	380	270	290

(**B**) Digestions with *Ban* I. A = blue marlin, sailfish, black marlin, spearfish; B = striped marlin, white marlin, spearfish; C = swordfish.

A	B	C
850	1500	700
650	400	650
400		400

nation of *Ban* I and *Hae* III was found to be diagnostic and to reveal a low level of intraspecific variation.

After finding diagnostic enzymes for use with the ND4 region, a total of 540 billfish samples was screened (Table 1) to evaluate the accuracy of the marker. Samples from a broad geographic range, including both the Atlantic and Indo-Pacific, were used for each species whenever possible. Of these, the white marlin, spearfishes and sailfish each exhibited one alternative restriction pattern for *Hae* III at low frequency (3.6%, 20.0% and 7.4% respectively) but in no case was the alternate pattern the same as a pattern seen in another species (Table 3). In addition, spearfishes exhibited an alternate pattern for the enzyme *Ban* I at a frequency of 40%; however, because *Ban* I was used only to discriminate white and striped marlin from sailfish in the ND4 identification key, this pattern did not affect the results (Figs. 1 and 2).

Nuclear marker

Six nuclear markers were screened in the preliminary analysis (Table 2). These included the short actin intron, the internal transcribed spacer (ITS) region (Goggin, 1994), and four anonymous single copy nuclear (scnDNA) markers. The scnDNA markers MN32-2, BM47, BM81, and WM08 were originally developed for analyses of popu-

lation structure in blue marlin (Buonaccorsi et al., 1999). The short actin intron primers were modified from "universal" actin gene primers "480" and "483" (Siddall et al., 2001).

Both the short actin and the ITS marker were rejected because neither marker amplified reliably across species. For the scnDNA markers, the program GeneJockey (Taylor, 1996) was used to search for the presence of restriction sites in sequences previously generated for blue marlin. The WM08 marker was screened with a total of ten enzymes, each of which produced identical patterns across species. BM47 and BM81 were also screened with ten enzymes each. For BM47, the combination of enzymes *Bcl* I and *Dde* I appeared to be diagnostic in a preliminary screening. However, upon further analysis, it was discovered that this combination of locus and enzymes produced confounding patterns for blue marlin and sailfish; the most common pattern for blue marlin was seen as a rare pattern for sailfish. Likewise, the BM81 locus did not distinguish between blue marlin and sailfish or between white and striped marlin and spearfish with any of the enzymes used. The MN32-2 locus was screened with a total of nine restriction endonucleases. The combination of *Dra* I and *Dde* I was found to allow for unambiguous identification of billfish species (Figs. 3 and 4).

As with the ND4 locus, after determining a diagnostic enzyme-locus combination, we screened a total of 540 billfish samples from a broad geographic range to evaluate the accuracy of the marker (Table 1). The enzyme *Dra* I was found to have two alternate alleles: "D" and "E" for blue marlin at a frequency of 19% and 5.5%, respectively. All other species appeared to be fixed for different (homozygous) alleles with respect to this enzyme. For *Dde* I, spearfishes had an alternate allele, "E," at a frequency of 36%. In addition, blue marlin had two alternate alleles "H" and "I" at frequencies of 16% and 40%, respectively (Table 4). Although the "H" allele in blue marlin was the only allele seen in black marlin, use of *Dde* I was not necessary to distinguish the two species since they are easily differentiated by *Dra* I (Figs. 3 and 4). All other species appeared to be homozygous for different alleles.

Figure 2

Key to distinguish species of billfishes based on the mitochondrial locus ND4.

Table 4

Restriction fragment patterns of the nuclear gene region BM32-2 of istiophorid billfishes. This locus did not amplify in the swordfish.

(**A**) Digestions with *Dra* I. A = blue marlin; B = striped marlin, white marlin, sailfish, black marlin; C = spearfish; D = blue marlin; E = blue marlin. A/D and A/E heterozygotes were seen in blue marlin cut with *Dra* I. Individuals of all other species were fixed homozygous.

A	B	C	D	E
650	640	640	650	1200
450	280	280	400	
	260	220	50	

(**B**) Digestions with *Dde* I. A = blue marlin; B = striped marlin, white marlin; C = spearfish; D = sailfish; E = spearfish; H = blue marlin; I = blue marlin. A/I A/H and H/I heterozygotes were seen in blue marlin cut with *Dde* I. C/E heterozygotes were seen in spearfish cut with *Dde* I. Individuals of all other species were fixed homozygous.

A	B	C	D	E	H	I
700	850	700	475	475	775	700
300	425	475	370	370	425	425
125		125	280	205		125
			130	125		

Discussion

The purpose of this study was to develop a key to the identification of billfish species based on independent mitochondrial and nuclear markers. Our goal was to make the process streamlined and capable of being performed in a modestly equipped genetics laboratory. Specific identification can be accomplished with a single PCR amplification of either the mitochondrial ND4 locus or nuclear MN32-2 locus and two restriction digestions. Previous methods with other mitochondrial gene regions have required the use of either four or 13 restriction digestions (Innes et al., 1998 and Chow 1994, respectively).

To facilitate specific identification, an objective of this study, was to develop diagnostic markers that exhibited limited intraspecific variation. Analysis of large sample sizes (60–100 or more) of sailfish, white marlin, striped marlin, blue marlin, and black marlin from throughout each species' range revealed minimal variation of the species-specific characters. Most species displayed a single genotype for digestions with the two enzymes used to cleave either the mitochondrial or nuclear amplification products, and no species exhibited more than three genotypes for any locus-restriction enzyme combination. In

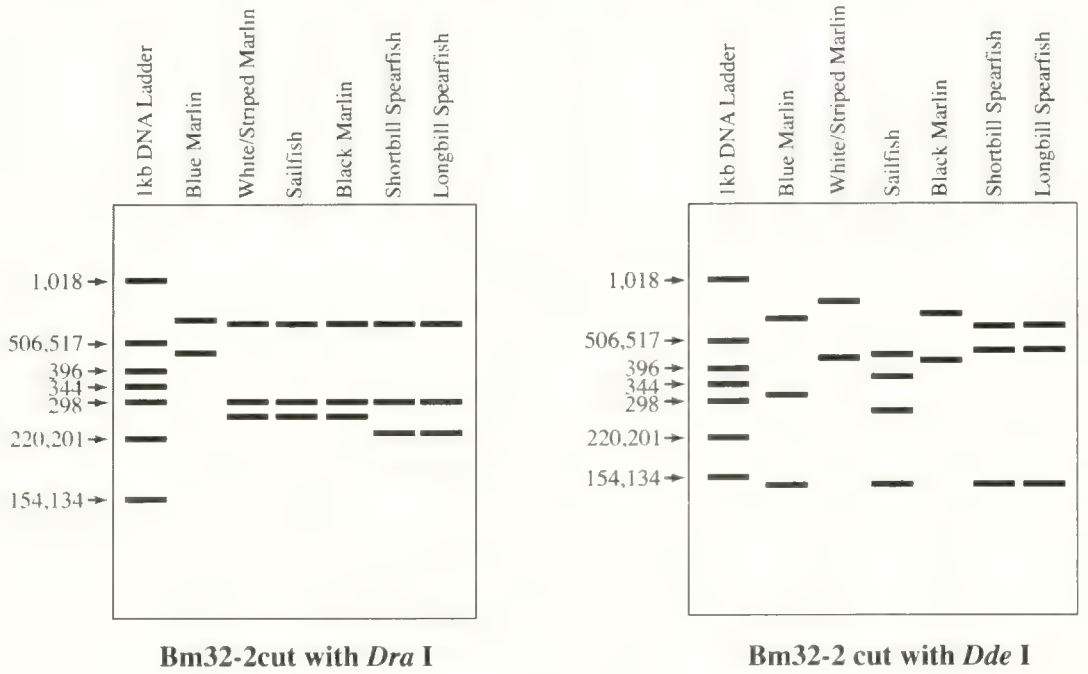

Figure 3

BM32-2 gel. Most common restriction fragment patterns of the nuclear gene region BM32-2 of istiophorid billfishes. This locus did not amplify in the swordfish. (**A**) Digestions with *Dra* I. From left to right, 1-kb DNA ladder, blue marlin (pattern A), white and striped marlin (pattern B), sailfish (pattern B), black marlin (pattern B), shortbill spearfish (pattern C), and longbill spearfish (pattern C). (**B**) Digestions with *Dde* I. From left to right, 1-kb DNA ladder, blue marlin (pattern A), white and striped marlin (pattern B), sailfish (pattern D), black marlin (pattern H), shortbill spearfish (pattern C), and longbill spearfish (pattern C).

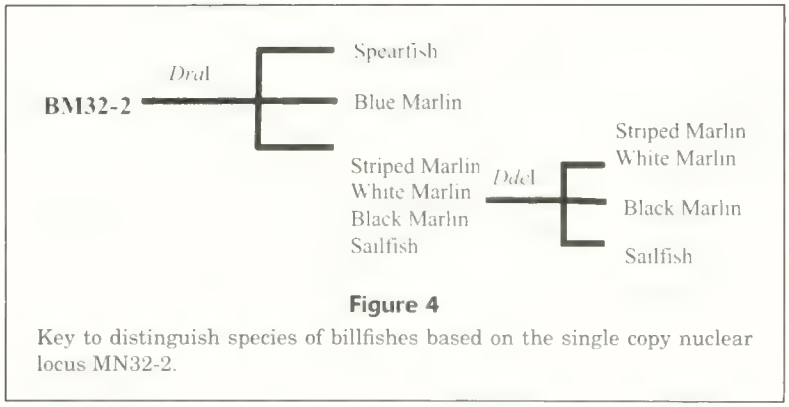

Figure 4

Key to distinguish species of billfishes based on the single copy nuclear locus MN32-2.

contrast, Innes et al. (1998) reported ten composite haplotypes among 47 black marlin, six composite haplotypes among 26 blue marlin, six composite haplotypes among 46 striped marlin, and six haplotypes among 21 swordfish, all from the southwest Pacific. From the level of intraspecific variation in relation to the sample sizes and the regional nature of their collections, it is reasonable to assume that Innes et al. (1998) may have missed several composite genotypes characteristic of the different species. In fact, from the level of variation exhibited by black marlin, striped marlin, and swordfish, Innes et al. (1998) suggested that their diagnostic species markers could be of potential use in population structure analyses. It occurs to us that if a genetic character exhibits sufficient intraspecific variation to be useful for analyses of stock structure, it is probably not a good candidate for species identification.

A high degree of genetic similarity was noted among white marlin and striped marlin in our study. None of the molecular markers evaluated in this study was able to unambiguously distinguish between the two species.

Figure 5

Larval billfish and its corresponding specific identification as a sailfish based on the BM32-2 locus. Lane 1 *Dra* I, lane 2, 1-kb plus DNA ladder (Gibco/BRL Life Technologies Inc., Bethesda MD), lane 3, *Dde I*.

Chow (1994) was also unable to distinguish between the two species based on RFLP analysis of the cytochrome *b* gene, and Innes et al. (1998) did not consider white marlin in their investigation because it does not occur in Australian waters. RFLP analysis of the whole mtDNA molecule indicated that white and striped marlin share composite haplotypes, although there are highly significant frequency differences between the species (Graves and McDowell, 1995; Graves, 1998). Sequence analysis of the mtDNA cytochrome *b* gene also demonstrated a lack of genetic divergence among white and striped marlin (Finnerty and Block, 1995), and a further genetic analysis of the species' relationships is warranted.

To evaluate the utility of the methods outlined in our study with those of other investigators, detailed protocols and six unknown billfish samples were sent to the Southeast Fisheries Science Center's (now National Ocean Survey's) Charleston, SC, laboratory. Scientists at the Charleston Laboratory analyzed both mitochondrial and nuclear DNA markers for each sample and arrived at consistent, correct identifications for each of the samples of unknown billfish. In addition, samples of juvenile billfish collected by investigators at the University of Miami were analyzed in our laboratory with these molecular markers. Samples consisting of one eye taken from a 3-mm juvenile billfish provided sufficient DNA to amplify the mtDNA and nuclear markers, allowing specific identification (Fig. 5). The technique is currently being used to determine the temporal occurrence of istiophorid larvae in the Florida Straits (Luthy and McDowell[2]).

Although the methods presented in our study allow the specific identification of billfish species, more sensitive molecular markers are required to distinguish among ocean populations of some istiophorid species. Amendment I to the Fishery Management Plan for Atlantic Billfishes prohibits the sale of blue marlin, white marlin, and sailfish taken in the Atlantic Ocean, although it is legal to market blue marlin, striped marlin, and sailfish from the Indian or Pacific oceans. Enforcement of this regulation requires the ability to discriminate between Atlantic and Indo-Pacific individuals of blue marlin, sailfish, and white and striped marlin. Examination of our results suggests that there are several other molecular markers, which while not used in this study, occur at relatively high frequencies in Atlantic blue marlin, sailfish, and white marlin but do not occur in their Pacific conspecifics. These molecular markers could potentially be used to identify some Atlantic individuals without misclassifying a Pacific fish, thereby allowing the enforcement of the management plan. Additional work will be required to develop a database that would support such analyses.

Acknowledgments

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Seasonal growth of King George whiting (*Sillaginodes punctata*) estimated from length-at-age samples of the legal-size harvest

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Abstract—Samples of 11,000 King George whiting (*Sillaginodes punctata*) from the South Australian commercial and recreational catch, supplemented by research samples, were aged from otoliths. Samples were analyzed from three coastal regions and by sex. Most sampling was undertaken at fish processing plants, from which only fish longer than the legal minimum length were obtained. A left-truncated normal distribution of lengths at monthly age was therefore employed as model likelihood. Mean length-at-monthly-age was described by a generalized von Bertalanffy formula with sinusoidal seasonality. Likelihood standard deviation was modeled to vary allometrically with mean length. A range of related formulas (with 6 to 8 parameters) for seasonal mean length at age were compared. In addition to likelihood ratio tests of relative fit, model selection criteria were a minimum occurrence of high uncertainties (>20% SE), of high correlations (>0.9, >0.95, and >0.99) and of parameter estimates at their biological limits, and we sought a model with a minimum number of parameters. A generalized von Bertalanffy formula with t_0 fixed at 0 was chosen. The truncated likelihood alleviated the overestimation bias of mean length at age that would otherwise accrue from catch samples being restricted to legal sizes.

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In this study, we estimated growth curves from six data sets of fish sampled from the commercial and recreational catch of an important fish species in South Australia (Fig. 1), King George whiting (*Sillaginodes punctata*). Like many temperate fish populations, recruitment and growth can be assumed to follow a yearly cycle. A variety of methods have been used to measure seasonal variation in fish growth including mark-recapture (Francis, 1988; Coggan, 1997) and otolith annulus-diameter increments in combination with tetracycline marking (Panfili et al., 1994; Fabré and St. Paul, 1998; Francis et al., 1999). The method used in our study is the most widely employed, of fitting to lengths-at-age, where the age of each sampled fish is read as a count of yearly otolith annuli from samples of the harvest.

The model-fitting algorithm had three key objectives, each to represent a specific feature of the growth of South Australian King George whiting, or of the data set. These were expressed mathematically as deviations from a standard 3-parameter von Bertalanffy model fitted with a normal likelihood.

The first two objectives were elaborations on the standard von Bertalanffy growth curve (understood as a deterministic function of mean length versus age). The first objective was to make seasonality explicit in the growth curve (Pitcher and MacDonald, 1973; Somers, 1988; Hoenig and Hanumara, 1990; Pauly and Gaschütz[1]) and the second objective was to allow a wider range of curvatures by using the *r*-exponent (Schnute, 1981).

For application of this growth description in length- and age-based stock assessment modeling, we also estimated the shape of the length-at-age probability density function (pdf), which quantifies the distribution of fish of different lengths at each age.

The principal regulation of both recreational and commercial King George whiting harvest is by legal minimum length (LML); fish smaller than the LML cannot be landed and must be returned to the sea. Therefore fish obtained from the catch are a biased sample. The third objective was to explicitly account for the absence of fish below the LML, for which a truncated pdf was used. This truncated normal density, the pdf of observed lengths-at-age, was also used as the likelihood for each individual sample.

A range of models were examined that met these three objectives. These included a seasonal version of the Richards (1959) model proposed by Akamine (1993), which makes different use of the *r*-exponent. Therefore a fourth objective was to apply standard statistical model selection techniques. Methods to choose the most appropriate model for a given growth data set were reviewed by Quinn and Deriso (1999). Hierarchical model fits are statistically comparable using their likeli-

[1] Pauly, D., and G. Gaschütz. 1979. A simple method for fitting oscillating length growth data, with a program for pocket calculators. Demersal Fish Committee, ICES council meeting 1979/G:24. ICES, Palægade 2-4 DK-1261 Copenhagen K, Denmark.

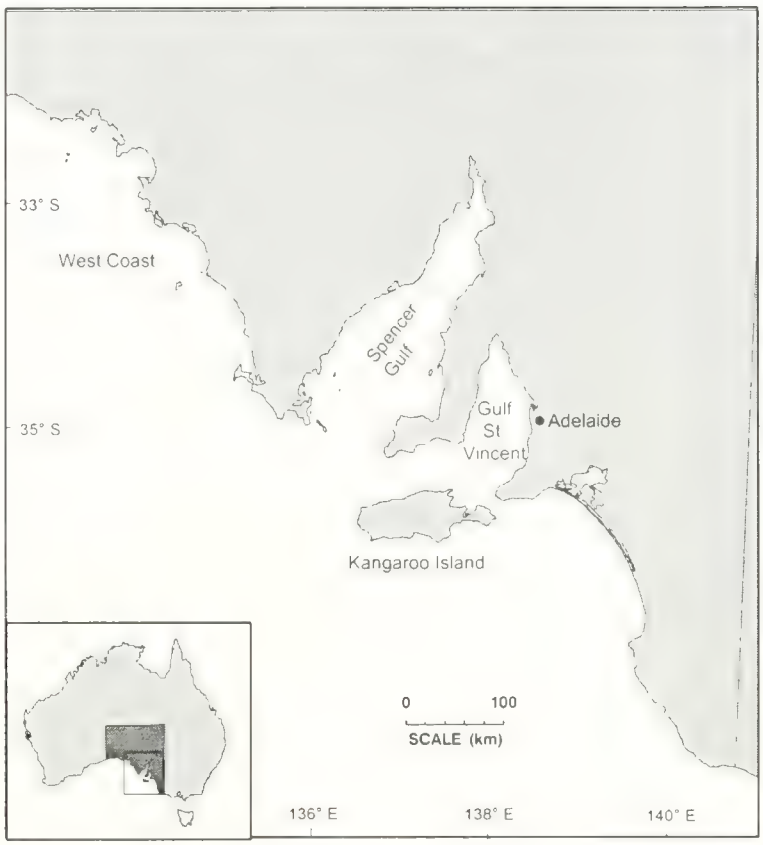

Figure 1

South Australian coastal waters. King George whiting (*Sillaginodes punctata*) are found predominantly in the two Gulfs, and along the West Coast.

hood ratio (Kimura, 1980; Rice, 1995). We sought to reduce the original 8-parameter model and employed likelihood ratio tests to evaluate the relative fit of the simpler models tested. We specify and apply a set of selection criteria below, seeking one common model form for six data sets to describe the length-at-age distributions. A 7-parameter generalized seasonal von Bertalanffy model, with t_0 fixed at zero, was chosen.

In addition, we applied an allometric relationship (a power curve) to fit weight versus length for this population.

That the samples are not uniform by length in commercial catch is common to most fisheries. The absence of fish below LML or below the lengths selected by the fishing gear, inevitable when sampling is from the landed catch, creates an overestimation bias of mean length-at-age, because faster growing fish reach the legal stock sooner and are thus over-represented in those samples. This sampling bias was taken into consideration by the use of a truncated model likelihood assuming zero probability of capture below legal size. In practice, the clear advantage of samples from the landed (commercial or recreational) harvest is a substantially lower cost than the alternative of fishery-independent samples gathered, usually by researchers, at sea.

The specific length-dependent bias in sampling changed during the time of the study. The LML was raised from 280 mm to 300 mm. Also, some of the samples were gathered by researchers who landed all, notably smaller fish. By applying one of three different likelihoods to any given sample, having different truncation lengths of 280 mm, 300 mm, or no truncation, all fish samples were combined in a single length-at-age estimation for each of three regional subpopulations, and by sex.

Materials and methods

A total of 11,164 King George whiting were sampled between 1995 and 1998 from across the main fishery area of South Australia. Most samples were obtained by subsampling the commercial catch at local fish processing plants or by purchasing fish from commercial processors. Some samples were provided as frozen fish frames (fillets removed) by recreational fishermen, and the remainder were caught on scientific cruises. Each fish was measured for total (TL) and standard lengths (SL) to the nearest mm, and weighed to 0.1 g. Gonads were removed, sexed, and weighed. The sagittae, the largest pair of otoliths, were removed from each fish for age determination.

Samples were subdivided into six data sets: three spatial regions and by sex (Table 1). Movement studies based

Table 1

Summary of data sets, each fish measured for age, length, and weight in the King George whiting analysis. Samples from commercial and recreational fisheries were regulated by a 280-mm legal minimum length (LML) before 1 September 1995, a 300-mm minimum length thereafter.

Area	Area abbreviation	Sex	Beginning date	End date	Sample size: Researchers	Fisheries 280 LML	Fisheries 300 LML
Gulf St. Vincent and nortern Kangaroo Island	GSV	male	4 Aug 94	17 Feb 99	293	503	1139
		female	4 Aug 94	17 Feb 99	373	615	1343
Spencer Gulf	SG	male	23 Apr 94	30 Sep 97	267	298	924
		female	23 Apr 94	30 Sep 97	363	441	1300
South Australian West Coast	WC	male	27 Apr 94	18 May 97	167	805	608
		female	27 Apr 94	19 May 97	226	857	642

on tag recoveries over three decades (Fowler and March[2]) indicated three largely self-sustaining subpopulations: Gulf St. Vincent, Spencer Gulf, and West Coast (Fig. 1).

Young fish (two- and three-year-olds) were aged by interpretation of the macrostructure of the whole sagittae. For fish with more complex otoliths, the otolith was snapped in two across the posterior-anterior axis through the center, exposing the transverse face of both halves. One of these halves was burnt in a bunsen flame and then examined with a binocular dissecting microscope at 6–20× magnification. The surface being examined was smeared with immersion oil. The alternating opaque and translucent zones were counted. The periodicity of formation of this macrostructure in sagittae of King George whiting has been validated and the following algorithm was developed for conversion of ring count to age (Fowler and Short, 1998):

$$a = 12N + m_b + m_c,$$

where a = age in months;
N = number of opaque zones;
m_b = 8 = number of months from universal birth date (i.e. 1 May) midway through spawning season to the end of the year; and
m_c = number of months from the start of year to the month of capture.

Some samples of fish were scaled in the commercial processing plant prior to weighing and measuring for length. Although this process did not affect their lengths, it did result in an appreciable loss of weight. Consequently, for estimation of weight-length relationships we corrected the weights of scaled fish using a linear relationship that was derived by weighing 155 fish before and after scaling. This linear relationship was

$$(corrected\ weight) = 1.0176 \times (scaled\ weight) + 3.5835\ (r^2=0.99, P<0.001, \mathrm{df}=154).$$

Growth: length-at-age

In order to make explicit the absence of fish samples smaller than LML, a truncated normal probability density function of length was used to describe the probability of capture of individual fish in each monthly age. This pdf was employed as the likelihood of observation of each individual, given its age. Truncation implies a zero predicted probability of observing a commercially or recreationally sampled fish less than LML. A few sublegal fish were measured and, being unrepresentative, were removed from the six data sets.

During the period of sampling, in September 1995, the regulated size of LML for commercial and recreational fishery samples was increased from 280 to 300 mm. The likelihood truncation length was thus a function of date of capture. This necessitated two forms of likelihood, for LMLs of 280 and 300 mm. Smaller numbers of samples obtained on scientific cruises were not subject to LML size controls. Thus a third, regular untruncated, likelihood was used to model research samples.

A normal likelihood was fitted to model the distribution of lengths at each age:

$$L \sim \frac{1}{\sqrt{2\pi}\,\sigma(a_i)} \exp\left[-\frac{1}{2}\left(\frac{l_i - \bar{l}(a_i)}{\sigma(a_i)}\right)^2\right], \qquad (1)$$

where l_i = length of fish sample i; and
a_i = age of fish sample i obtained from count of its otolith annuli.

[2] Fowler, A. J., and W. A. March. 2000. Adult movement patterns. *In* Development of an integrated fisheries management model for King George whiting (*Sillaginodes punctata*) in South Australia (A. J. Fowler and R. McGarvey, eds.), p. 83–104. FRDC Final Project Report 95/008. Fisheries Research and Development Corporation, PO Box 222, Deakin West ACT 2600, Australia.

The mean length-at-age

$$\bar{l}(a_i) = L_\infty \left\{ 1 - \exp\left[K \left\langle \frac{a_i - t_0}{12} + \frac{u}{2\pi} \left| \frac{\sin(2\pi(a_i - \omega)/12) - \left| \sin(2\pi(t_0 - \omega)/12) \right|}{} \right| \right\rangle^r \right] \right\}, \quad (2)$$

was modeled by a seasonally periodic von Bertalanffy growth formula, generalized by the inclusion of an exponent, r. Age (a_i) was in integral units of months, with May, the assumed date of birth at mean time of spawning of South Australian King George whiting, being month 1. Division by 12 in the mean length formula preserves the usual units of K where age is in years.

The seasonality function is sinusoidal, although more complex seasonality functions can be postulated that allow asymmetry in growth through the year. Values of the seasonality amplitude parameter $u > 1$ imply decreasing length in the yearly time of minimum growth (Pauly and Gaschütz[1]). We therefore constrained $u \leq 1$, assuming that no shrinking in length occurs. With sine, the phase parameter (ω) gives the month of maximum growth, where months of age 1, 13, 25, etc. denote the birth month, May.

The likelihood standard deviation (σ) was modeled as an allometric function of mean length:

$$\sigma(a_i) = s_0 \left(\bar{l}(a_i)\right)^{s_1}. \quad (3)$$

This power function for standard deviation in terms of mean length, applied by Francis (1988) to fitting tag-recovery length increments, has the desired property that once growth stops, the standard deviation in lengths-at-age also ceases to change. Similarly, in winter months of slowed (or zero) mean length increase, change in standard deviation slows correspondingly.

The left-truncated normal likelihood, which applies to samples from commercial and recreational fishermen,

$$L_i = \begin{cases} \dfrac{1}{\sigma(a_i)} \exp\left[-\frac{1}{2} \left| \dfrac{l_i - \bar{l}(a_i)}{\sigma(a_i)} \right|^2 \right] \Bigg/ \\ \left\{ \displaystyle\int_{LML_i}^{\infty} \frac{1}{\sigma(a_i)} \exp\left[-\frac{1}{2} \left| \frac{l - \bar{l}(a_i)}{\sigma(a_i)} \right|^2 \right] dl \right\}, \text{ if } l_i \geq LML_i \\ 0, \text{ if } l_i < LML_i \end{cases} \quad (4)$$

postulates a probability cut-off to zero for landed samples less than LML and a normal probability, integrating to 1, for the range of legal lengths. LML is subscripted by the fish sample data point (i) to indicate that LML is either 280 or 300 mm depending on the date of capture of the fish. For research samples, for which all lengths could be observed, the full untruncated normal likelihood (Eq. 1) was used.

Parameters were estimated by minimizing the negative sum of log-likelihoods with the AD Model Builder estimation software (Otter Research Ltd., Sidney, B.C., Canada):

$$O = -\sum_{i=1}^{n} \ln(L_i). \quad (5)$$

Initial parameter values for all models tested were $t_0 = 0$, $u = 1$, $\omega = 9$, $s_0 = 0.1$, $s_1 = 1$, $r = 1$, with $L_\infty = 480$, $K = 0.36$ for females, and $L_\infty = 420$, $K = 0.6$ for males.

Confidence bounds on parameters for each data set were derived by assuming the standard asymptotic normal approximation. These were numerically calculated by AD Model Builder routines as the diagonal elements of the covariance matrix, the negative inverse of the Hessian matrix at the likelihood maximum.

Growth model choice

The full, seasonal, generalized von Bertalanffy model described above has eight parameters. A best-fitting model with the minimum number of parameters was sought. In cases where a model is overparameterized, high correlations between parameters appear and the confidence bounds widen. To test for a diagnosis of overparameterization and then to correct it by fixing otherwise freely estimated parameters, we applied the following algorithm based on standard methods of model selection:

1 Search for parameters that frequently show high correlations with other parameters, have high variances, or in estimation hit preset upper and lower bounds, beyond which biologically unrealistic values are being inferred.
2 Set those parameters to fixed likely values. This assumes a biologically likely value can be postulated. If not, use a mean value among the range of estimates obtained when the parameter is allowed to vary freely. A parameter may also be selected if it varies little among the range of data sets for which estimates are obtained.
3 Test for the change in negative log-likelihood to determine whether the reduced model is significantly less well fitting by using chi-square likelihood ratios.
4 Check that confidence intervals and correlations are reduced.

In addition, we seek model that converges reliably for all data sets. Satisfactory convergence should not depend on the initial parameter values chosen, but in some cases a new set of initial values can be tried for any given nonconverging data set. Convergence can also depend on the minimization algorithm or subroutine employed. However, for purposes of model selection, failure to converge for some data sets analyzed is an indication that the likelihood surface for that model is less smooth and the true global maximum may not always be obtained. Reliable convergence is particularly desirable when 1) bootstrapping, where nonconvergence leaves resampled data sets

unestimated, and 2) for integration of growth into overall fishery stock assessment estimators, where finding more appropriate initial values for the growth parameters may be nontrivial, and the cause of nonconvergence of the overall estimation may not be easily traced to the growth submodel.

In addition to reduced versions of the model presented above, we fitted a related model proposed by Akamine (1993), which incorporates into the Richards (1959) growth curve a sinusoidal seasonality function like that of Equation 2.

Weight-at-length

Mean (corrected) weight versus total length was modeled by an allometric relationship:

$$\overline{w}(l_t) = \alpha l_t^{\beta} \tag{6}$$

A normal likelihood was again used. The standard deviation of the likelihood (i.e. of the fitted spread of observed weights about the mean given in Eq. 6) was assumed to vary linearly with length:

$$\sigma_w(l_t) = \sigma_{w0} + \sigma_{w1} l_t, \tag{7}$$

Parameter confidence bounds were estimated by a bootstrap of 1000 runs.

Results

Growth model choice

The generalized von Bertalanffy model (Eq. 2, abbreviated as gVB) gave the best fit with five of six data sets (Table 2). However for both gVB and the other 8-parameter model, Akamine-Richards (AR), correlations among parameters were unacceptably frequent and high (Table 2). Other evidence of overparameterization included frequent occurrence of wide confidence bounds (SE >20%, Table 2). High correlations and parameter uncertainties were most widespread for s_0 and s_1. The exponent, r, and seasonality amplitude, u, also occurred frequently with high uncertainty, and t_0 and r often were found in high correlations; t_0 hit both upper (7.99) and lower (–30) confidence bounds for some models with west coast data sets. As with standard von Bertalanffy models, t_0 quantifies the age (here, in months) at which length extrapolates to 0. The occurrence of u estimates hitting their upper bound of 1 is not due to model overparameterization but reflects the biological modeling decision to exclude shrinking.

The Akamine-Richards (AR) model varied widely among data sets in its relative closeness of fit, failed to converge for West Coast females, and did not yield a positive definite hessian for Gulf St. Vincent females. It was less well fitting than the gVB for all but one data set. The gVB model was therefore chosen as the better 8-parameter model, and subsequent reduced models were based on it in preference to AR.

From indicators summarized above, four parameters for defining overall mean length K, L_∞, t_0 and r, appear to be too many. Two obvious candidates for fixing to constant values were t_0 and r. These occurred frequently in indicators of model overparameterization. Both have intuitive biological default values at which they can be fixed, 0 and 1 respectively. Thus two 7-parameter models were run, with t_0 and r fixed, the latter (with r=1) reducing to a seasonal von Bertalanffy curve (Somers, 1988; Hoenig and Hanumara, 1990).

The fit with $t_0 = 0$ fixed was not significantly different from the full 8-parameter gVB for three of six data sets. This fit was tested by chi-square likelihood ratios at 95% confidence, indicated (Table 2) by successive likelihood-ratios of 1.92 or less, for comparing fits of hierarchical models differing by one in number of freely estimated parameters (Rice, 1995). The regular seasonal von Bertalanffy model (r=1, abbreviated as "reg VB") fitted less closely than gVB with $t_0 = 0$ for all six data sets; significantly worse for all Spencer Gulf and West Coast data sets. In addition, not shown in Table 2, the estimates of t_0 were frequently far from the realistic biological range near 0, often estimated at 10 to 20 months above or below. The frequency and magnitude of high correlations were substantially reduced with both 7-parameter models. Thus we choose to fix $t_0 = 0$ and let r freely vary.

The occurrence of very high correlation between s_0 and s_1 for all data sets and models (Table 2) suggested fixing one of them, in particular, the exponent, s_1. We set $s_1 = 0.3$ which fell near the average among the range of estimated values. The outcome was that t_0 (now free) hit its bound in three of six cases, thus exacerbating that pathology. When both $t_0 = 0$ and $s_1 = 0.3$ were fixed, the fits were uniformly poor (Table 2). Thus, the high correlation between the two allometric standard deviation parameters met with no obvious solution. However, these posed no wider problem because these parameters did not interact with those describing the mean length at age and the correlation between pairs of allometric parameters (such as α and β in the weight-length model, Eq. 6) is common and often unavoidable. Because a significantly better fit for the length-at-age standard deviation is sought, we let both s_0 and s_1 vary freely.

The gVB with $t_0 = 0$ fixed provided an optimal trade-off in reduced overparameterization and good fit: it achieved the objective of substantially reduced interparameter correlations without significantly worse fits in three of six cases. The remaining three data sets (Spencer Gulf females and males, West Coast females) had yielded unrealistic estimates of t_0 in full model gVB (of –17.9, –21.7, and the upper bound of 7.99 respectively). This model was therefore chosen and results from it presented below.

Growth: length-at-age

Estimated length at age showed seasonal periodic trends for the three regions and two sexes (Figs. 2–4). Estimates of u (seasonality amplitude) were constrained at the maximum allowed value of $u = 1$ for three of six data sets (Table 3). The peak month of maximum growth occurred in mid-

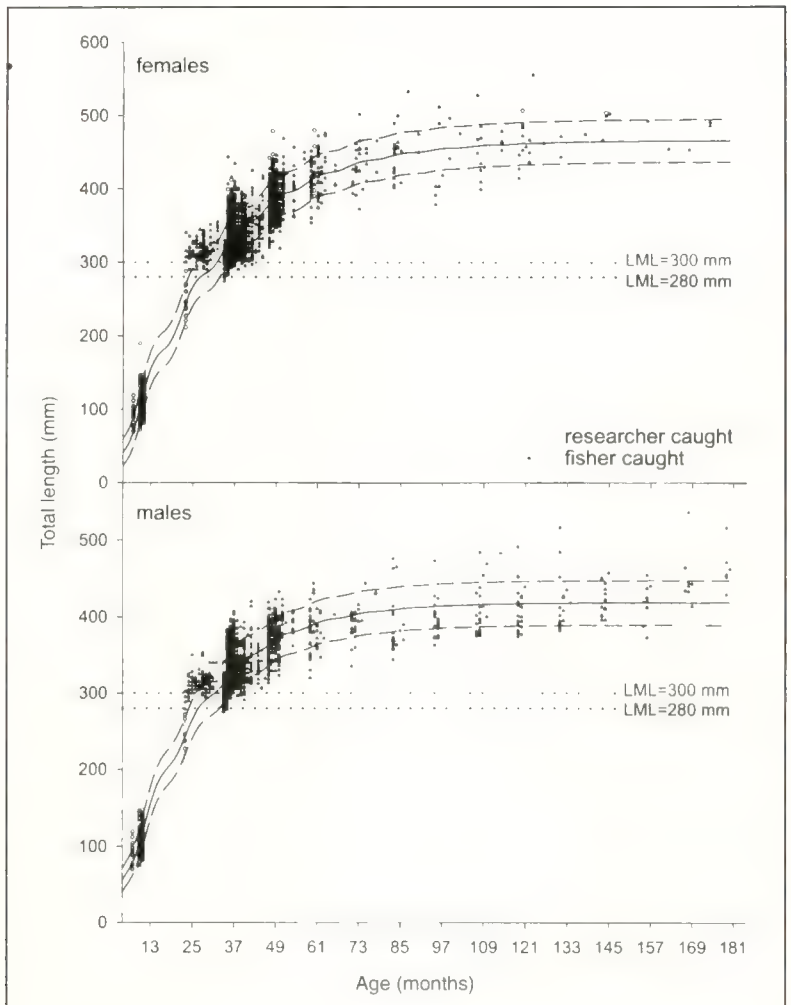

Figure 2

Lengths at age, beginning at 10 months, for Gulf St. Vincent King George whiting of both sexes. The solid line is the generalized seasonal von Bertalanffy mean length curve (Eq. 2) with $t_0 = 0$ fixed. Dashed lines indicate confidence bounds as normal likelihood standard deviation (Eq. 3). Dots represent individual observations of length-at-age.

summer (December–February) for all data sets except Gulf St. Vincent males.

Estimated (likelihood maximum) and observed distributions of lengths-at-age were plotted for Gulf St. Vincent females (Fig. 5) and males (Fig. 6). Because the estimation likelihood was fitted to formulas for mean (Eq. 2) and standard deviation (Eq. 3) of all ages at once, close fit to the majority of individual length-at-age distributions indicated a growth description mutually consistent among ages and a satisfactory approximation to monthly lengths at age overall.

For younger ages (28–35 months), the sampled frequencies were modeled by the truncated right-hand component of the normal pdf. The LML truncation lengths for each normal curve (280 or 300 mm in Figs. 5 and 6) indicated the lower limit of samples from the fishery. These samples are generally well fitted (Figs. 5 and 6), suggesting these truncated younger samples do contribute to the overall growth fit and that the truncated likelihood is effective in describing the monthly growth of the length-at-age cohort across LML into legal sizes. One exception yielding a less close fit were female fish aged 28 months taken under a LML of 280 mm (Fig. 5).

Weight-at-length

Parameter estimates for α and β (Eq. 6) covaried strongly. When all four parameters were allowed to freely vary, β differed little from 3.2 for all data sets (Table 4). Likelihood-ratio tests were therefore carried out to determine whether the model allowing β to vary freely yielded significantly better fits than one with three parameters and β fixed at 3.2. For all but Spencer Gulf males, likelihood-

Table 2

Criteria for model selection. gVB = generalized von Bertalanffy (Eq. 2); AR = Akamine-Richards (Akamine, 1993). Reduced gVB models fixed t_0 at 0 and s_1 at 0.3. Models in each data set are given in order of best to worst fitting. Differences in –logL provide likelihood ratio (L-ratio) test comparisons of the goodness of fit of successively reduced hierarchical models. An L-ratio of 1.92 (3.0) or greater implies a significantly better fit at 95% under a chi-square likelihood ratio test by comparison with reduced models of one (two) fewer parameters. High correlations between pairs of parameters are shown for three arbitrary categories: ** = >0.99; * = 0.95–0.99; pairs in this column unmarked by an asterisk had correlations of 0.9–0.95.

Data set	Model	No. of parameters	–logL	Successive L-ratios	Parameter pairs with |cors| >0.9	Parameters with SE/ estimate > 0.2	Parameters hitting estimation bound
Gulf St. Vincent females	gVB	8	10566.63		t_0~r**; t_0~K; r~K; s_1~s_0**	u, r, s_0, s_1	
	gVB t_0=0	7	10568.09	1.45	r~K; s_1~ s_0**	u, s_0, s_1	
	gVB t_0=0 & s_1=0.3	6	10570.38	2.29	r~K	u	
	reg VB	7	10571.27	0.89	L_∞~K; s_1~ s_0**	u, s_0, s_1	
	AR	8	10575.67	4.39	Hessian not positive definite	—	
Gulf St. Vincent males	gVB	8	8632.695		t_0~r**; t_0~K*; ω~K; s_1~ s_0**; t_0~ω*; r~K*; r~ω	u, r, s_0	
	AR	8	8632.695	0.00	t_0~r**; t_0~K*; r~K; s_1~ s_0**; t_0~ω*; ω~K; r~ω	u, r, s_0	
	gVB t_0=0	7	8632.759	0.06	r~K; s_1~ s_0**	u, s_0	
	reg VB	7	8632.908	0.15	t_0~u; s_1~ s_0**	u, s_0	
	gVB t_0=0 & s_1=0.3	6	8637.379	4.47	Hessian not positive definite	u	
Spencer Gulf females	gVB	8	9374.685		t_0~K; r~K; r~ t_0**; s_1~ s_0**	s_0, s_1	u=1
	gVB t_0=0	7	9391.099	16.41	K~ L_∞; r~K; s_1~ s_0**	s_0, s_1	u=1
	gVB t_0=0 & s_1=0.3	6	9392.176	1.08	K~ L_∞; r~K		
	AR	8	9420.834	28.66	K~ L_∞; s_1~ s_0**	s_0, s_1	u=1
	reg VB	7	9429.822	8.99	K~ L_∞; s_1~ s_0**	s_0, s_1	u=1
Spencer Gulf males	gVB	8	6620.955		t_0~r; s_1~ s_0**	r, s_0, s_1	u=1
	gVB t_0=0	7	6661.097	40.14	r~K; s_1~ s_0**	s_0, s_1	u=1
	AR	8	6728.644	67.55	K~ L_∞; s_1~ s_0**	s_0, s_1	u=1
	reg VB	7	6729.238	0.59	s_1~ s_0**	s_0, s_1	u=1
	gVB t_0=0 & s_1=0.3	6	7230.275	501.04	r~K	u	
West Coast females	AR	8	7771.561		K~ L_∞; r~ L_∞**; r~K*; s_1~ s_0**	s_0, s_1	t_0=-30
	gVB	8	7798.542	26.98	K~ L_∞; r~K; s_1~ s_0**	s_0, s_1	u=1
	gVB t_0=0	7	7805.209	6.67	K~ L_∞; r~K; s_1~ s_0**	s_0, s_1	u=1
	reg VB	7	7819.477	14.27	K~ L_∞*; s_1~ s_0**	s_0, s_1	u=1, t_∞=7.99
	gVB t_0=0 & s_1=0.3	6	7828.671	9.19	K~ L_∞; r~K*	u	
West Coast males	gVB	8	7011.73		r~K*; s_1~ s_0**	u, s_0, s_1	t_∞=7.99
	gVB t_0=0	7	7013.403	1.67	r~K*; r~u; s_1~ s_0**	u, r, s_0, s_1	
	reg VB	7	7083.513	70.11	K~ L_∞*; s_1~ s_0**		t_∞=7.99
	gVB t_0=0 & s_1=0.3	6	7828.671	745.16	r~K*; r~u	u, r	
	AR	8	failed to converge	—			

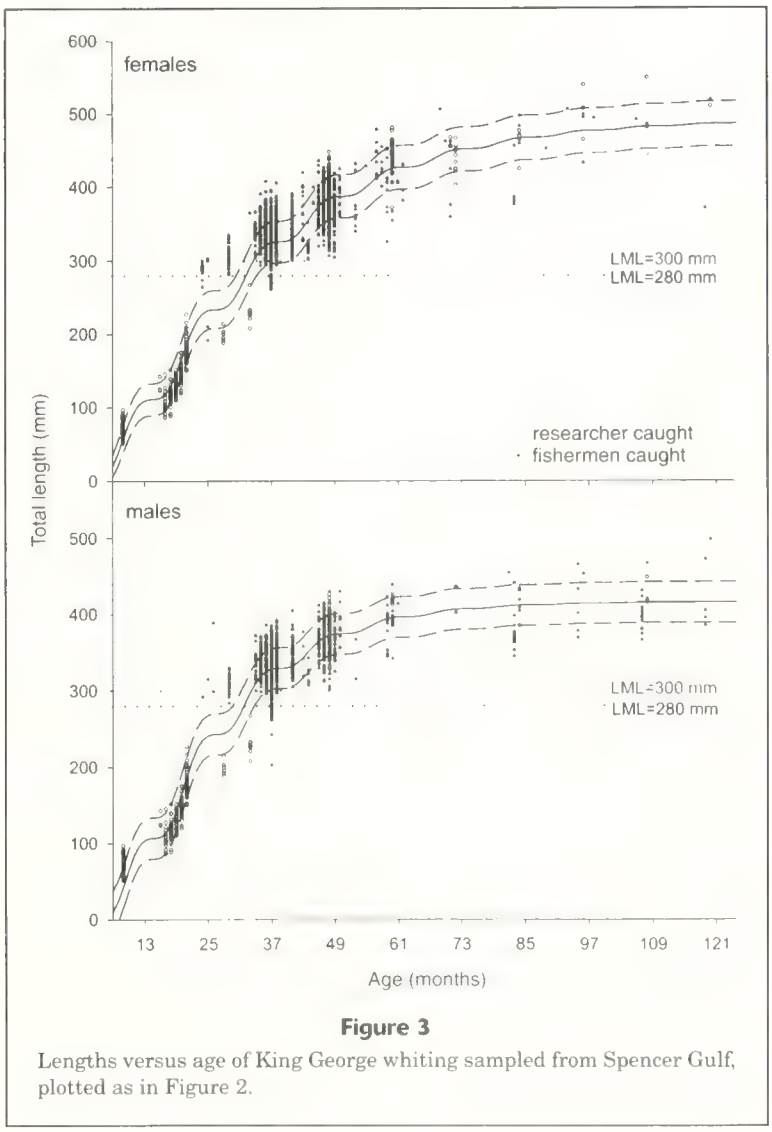

Figure 3

Lengths versus age of King George whiting sampled from Spencer Gulf, plotted as in Figure 2.

ratio tests showed that β did not differ significantly from 3.2 (Table 4). With $\beta = 3.2$ fixed, values of α among the six data sets differed little (Table 5, Fig. 7).

Discussion

In this study we estimated parameters of length at age for six data sets, comparing the fits of different models by using four standard diagnostic tools, notably likelihood ratios, correlations, standard errors, and parameter estimates among data sets either varying widely or varying little, to evaluate the estimators being compared. Similarly, for weight versus length in the same population, we assessed six data sets, and used likelihood ratio to compare model fits. For both length at age and weight versus length, the diagnostic analysis suggested the initial full models were overparameterized and indicated which parameters should be fixed and what values.

Likelihood ratio tests allow comparisons only between hierarchical models, that is in comparing full and reduced models, the latter a subcase of the full model obtained by fixing one or more parameters in the full model. In the case of generalized von Bertalanffy and Akamine-Richards, setting $r = 1$ yielded the same model, namely seasonal von Bertalanffy. The other two reduced models analyzed (gVB with t_0=0 and with both t_0=0 and s_1=0.3) were reduced models only of generalized von Bertalanffy. Although other comparison tests are possible for hierarchical models (Quinn and Deriso, 1999), the Neyman Pearson lemma assures that in the situation where it applies, the likelihood-ratio test is optimal in that it yields the most powerful test for any given choice of significance level, α (Rice, 1995).

Fits of nonhierarchical models can be compared by using the Akaike or Bayes information criteria (Quinn and Deriso, 1999). Fournier et al. (1998) applied the Aitkin posterior Bayes factors for hypothesis model comparisons in

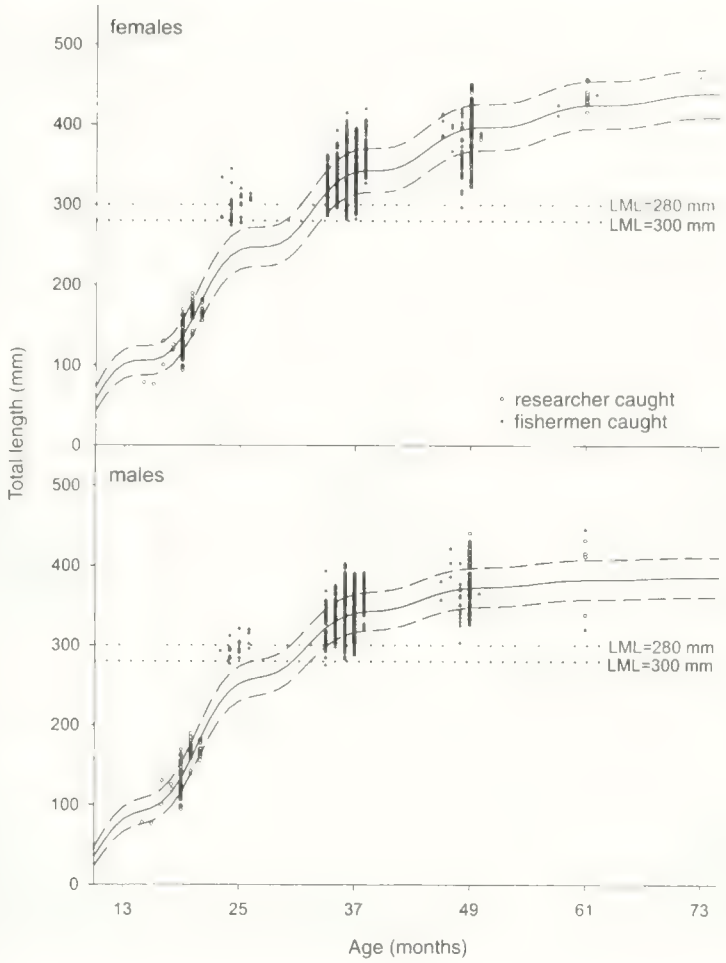

Figure 4

Lengths at age for the South Australian West Coast, plotted as in Figure 2.

a Bayesian context. Recently, Buckland et al. (1997) have proposed averaging the estimates from the range of models examined, weighting each estimate by functions of the Akaike or Bayes information criteria. This mitigates the need to choose one specific model as we have done, and like the Akaike or Bayes criteria, applies to nonhierarchically related models. However, in situations where the growth model will be incorporated into a larger stock assessment estimation, a range of growth submodels would be challenging to implement. Moreover in cases where evidence of overparameterization is given, a reduced-parameter model can reduce both bias and the influence of sample variation.

Sinusoidal seasonality (Pauly and Gaschütz[1]) was represented in a now standard way that preserves the interpretation of t_0 as the age at which length equals zero (Somers, 1988; Hoenig and Hanumara, 1990). Pawlak and Hanumara (1991) showed that this form of seasonality model yielded statistical advantage. Hyndes et al. (1998) aged samples of King George whiting in southwestern Australia that grew faster and reached larger maximum lengths than those from South Australia. The analysis of Hyndes et al. (1998) did not describe the distribution of lengths-at-age or consider seasonality, which was less evident in their plotted data.

The exponent, r, allowed nonlinear variation away from the strict von Bertalanffy form. With the South Australian King George whiting data sets, it improved the model description; fitted r's ranged from 1.25 to 4.59, outside the range describable by the unmodified seasonal von Bertalanffy model where implicitly $r = 1$ fixed.

We are not aware of previous attempts to use a truncated likelihood in an age-based description although Smith and Botsford (1998) applied size truncation in fitting a von Foerster equation to length samples. Truncation proved effective in alleviating this potential large source of bias. The extent of the bias is evident in the growth curve scatterplots (notably Figs. 2 and 4) where large numbers of

Table 3

Length-age parameters and derived estimates (with t_0=0 fixed). The 95% confidence intervals shown in parentheses are 1.96 times the asymptotic standard error; for strictly positive parameters, these are shown as percentages of the estimate value.

	Gulf St. Vincent		Spencer Gulf		West Coast	
Parameter	females	males	females	males	females	males
L_∞	467.0 (±1.5%)	418.4 (±1.1%)	492.6 (±2.2%)	416.1 (±1.5%)	454.4 (±3.2%)	387.0 (±2.8%)
K	0.48 (±6.4%)	0.61 (±5.8%)	0.49 (±6.9%)	0.77 (±6.6%)	0.70 (±9.4%)	1.17 (±15%)
u	0.59 (±41%)	0.46 (±68%)	1 (±0.05%)	1 (±0.08%)	1 (±0.14%)	0.79 (±57%)
ω	–1.55 (Feb) (±0.77)	24.0 (Apr) (±0.004)	8.50 (Dec) (±0.32)	8.67 (Dec) (±0.39)	8.96 (Dec) (±0.42)	9.02 (Jan) (±0.59)
s_0	8.97 (±58%)	4.17 (±47%)	7.34 (±52%)	27.6 (±53%)	3.53 (±96%)	3.93 (±100%)
s_1	0.19 (±0.10)	0.32 (±0.082)	0.23 (±0.091)	-0.005 (±0.095)	0.35 (±0.17)	0.31 (±0.17)
r	1.25 (±6.9%)	1.41 (±7.8%)	1.66 (±6.9%)	2.35 (±9.8%)	2.33 (±11%)	4.59 (±40%)

Table 4

Likelihood-ratio tests comparing differences in the fits between weight-length models which allow β to vary and those which kept $\beta = 3.2$ fixed. Significant difference is indicated by $P < 0.05$.

	Gulf St. Vincent		Spencer Gulf		West Coast	
	females	males	females	males	females	males
β-estimate (free to vary)	3.200255	3.200008	3.200031	3.198721	3.200050	3.200021
L-ratio statistic	0.677	0.000	0.005	6.094	0.033	0.006
P-significance (models differ)	0.41	0.99	0.94	0.01*	0.86	0.94

Table 5

Weight (g) versus length (mm TL) parameters from Equation 6 and derived estimates with $\beta = 3.2$ fixed. 95% confidence intervals are 1.96 times the bootstrap standard deviation over 1000 runs given in parentheses as percentages of the estimate value.

	Gulf St. Vincent		Spencer Gulf		West Coast	
Parameter	females	males	females	males	females	males
α	$1.858–10^{-6}$ (±0.51%)	$1.874–10^{-6}$ (±0.63%)	$1.880–10^{-6}$ (±0.77%)	$1.888–10^{-6}$ (±0.87%)	$1.861–10^{-6}$ (±0.40%)	$1.887–10^{-6}$ (±0.32%)
β	3.2	3.2	3.2	3.2	3.2	3.2
σ_{u0}	–7.76 (±15%)	–6.74 (±12%)	–6.94 (±13%)	–5.21 (±24%)	–6.38 (±13%)	–6.32 (±6.2%)
σ_{u1}	0.094 (±8.0%)	0.080 (±7.2%)	0.087 (±12%)	0.078 (±19%)	0.067 (±8.0%)	0.063 (±4.6%)

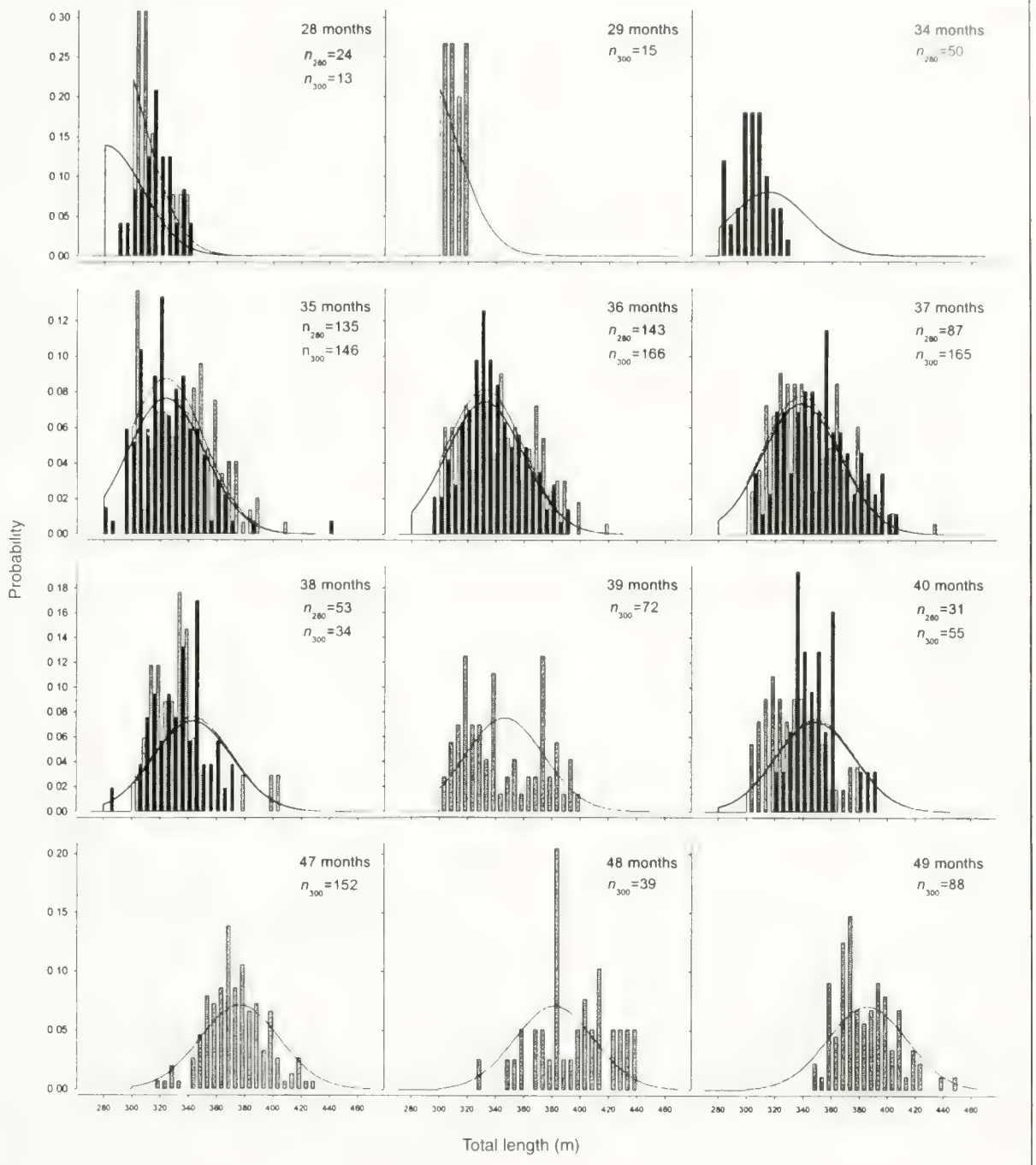

Figure 5

Female Gulf St. Vincent length-frequency histograms expressed as proportion of fish caught per 5-mm length class. Ages (by month) illustrated were those of largest sample size. Black bars correspond to fish caught when the fishery was subject to a 280-mm size limit, and gray bars for fish caught under a 300-mm size limit. The fitted normal likelihood probability density curves (Eq. 4) calculated for each size limit have been overlaid for comparison.

samples were obtained in the ages (~30 months) at which the faster fish are entering the legal-size stock. These clumps of points lie well above the estimated mean length at age. In the absence of the truncation method, the mean curves would pass through these points.

Only the Akamine-Richards model failed to converge with the South Australian King George whiting data sets. Because the Richards form of the model includes both the exponent and its inverse in different places in the formula, it is likely to result in a more numerically challenging

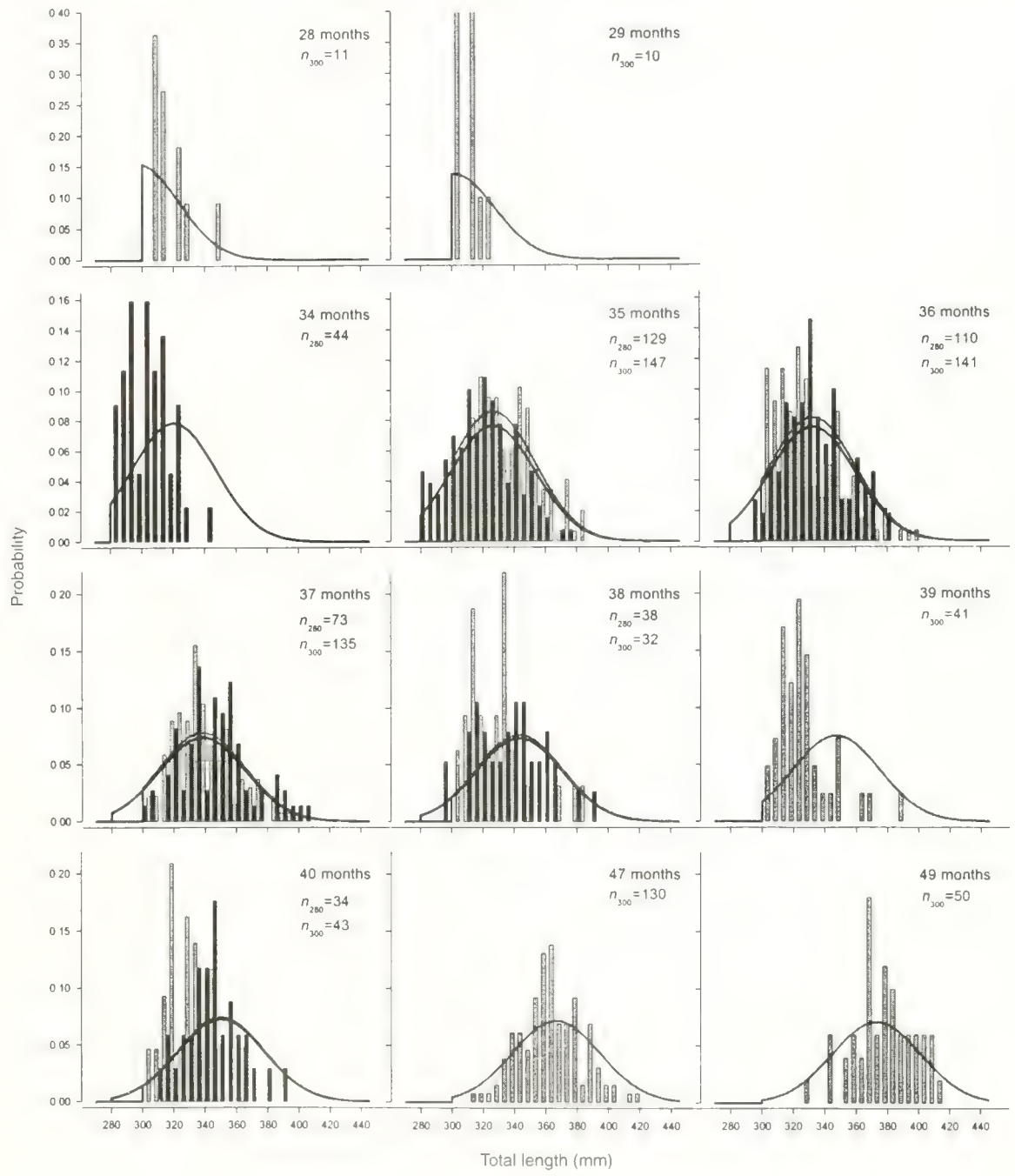

Figure 6

Male Gulf St. Vincent length-frequency histograms and fitted truncated normal density curves, as in Figure 5.

minimization algorithm. The two occurrences of the parameter, r, in the Richards formula $L = L_\infty/\{1 + re^{-K(t-t_0)}\}^{1/r}$, as a factor in front of the negative exponential and as its reciprocal exponent around the entire function apart from L_∞ can act in contrary fashion. For $r > 1$, increases in r imply an increase in length-at-age because of the parameter as a reciprocal exponent, and the opposite for the second role the parameter plays in describing mean length. We speculate that the Richards growth formula was less numerically robust because r can rise and fall at different parameter ranges along the path to convergence, resulting in a more complex likelihood surface.

Modeling the full length distribution at each monthly age is valuable for assessing populations of heavily ex-

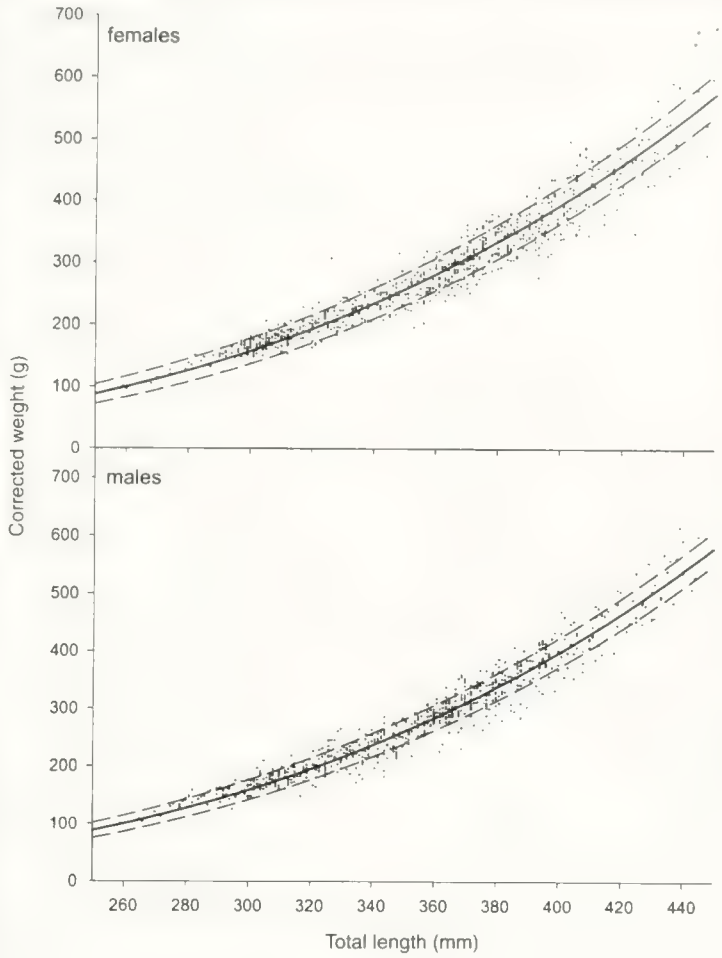

Figure 7

Allometric length versus weight relationship (Eq. 6), fitted to Gulf St Vincent samples. Weights for some fish samples are corrected for the removal of scales before weighing. Error bars (dashed lines) indicate normal likelihood standard deviation (Eq. 7).

ploited species such as King George whiting where depletion of the legal sizes of the cohort is rapid over monthly time scales. In fishery stock assessment models where only legal-size lengths of each yearly cohort are subject to exploitation and where size selection is driven primarily by a legal size limit rather than size-varying gear selectivity, model accuracy is improved by dividing the cohort length distribution into legal and sublegal components.

Growth was variable, reflected in high standard deviations in lengths-at-age of King George whiting. This meant a time span of 12–24 months between the crossing into legal size of the first (i.e. fastest growing, at ~23 months of age) and last 2% of the normal cohort to reach LML. Because fishing mortalities are such that a majority of fish are removed within 24 months of reaching legal size, the explicit representation of the distribution of harvestable lengths of cohorts as they cross LML allows substantial improvements in stock assessment, notably in fitting only legal sizes to monthly catch totals by weight and sampled numbers at age. Moreover, the seasonal variations in fishing effort targeted on South Australian King George whiting appear to track the arrival of the bulk of recruits to legal size in autumn and early winter. The growth model presented in our study allowed this feature of seasonal timing in recruitment to be captured in the associated stock assessment population model.

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Abstract—We analyzed data from National Marine Fisheries Service bottom trawl surveys carried out triennially from 1984 to 1996 in the Gulf of Alaska (GOA). The continental shelf and upper slope (0–500 m) of the GOA support a rich demersal fish fauna dominated by arrowtooth flounder (*Atheresthes stomias*), walleye pollock (*Theragra chalcogramma*), Pacific cod (*Gadus macrocephalus*), Pacific halibut (*Hippoglossus stenolepis*), and Pacific Ocean perch (*Sebastes alutus*). Average catch per unit of effort (CPUE) of all groundfish species combined increased with depth and had a significant peak near the shelf break at 150–200 m. Species richness and diversity had significant peaks at 200–300 m. The western GOA was characterized by higher CPUEs and lower species richness and diversity than the eastern GOA. Highest CPUEs were observed in Shelikof Strait, along the shelf break and upper slope south of Kodiak Island, and on the banks and in the gullies northeast of Kodiak Island. Significant differences in total CPUE among surveys suggest a 40% increase in total groundfish biomass between 1984 and 1996. A multivariate analysis of the CPUE of 72 groundfish taxa revealed strong gradients in species composition with depth and from east to west, and a weak but significant trend in species composition over time. The trend over time was associated with increases in the frequency of occurrence and CPUE of at least eight taxa, including skates (Rajidae), capelin (*Mallotus villosus*), three flatfish species, and Pacific Ocean perch, and decreases in frequency of occurrence and CPUE of several sculpin (*Myoxocephalus* spp.) species. Results are discussed in terms of spatial and temporal patterns in productivity and in the context of their ecological and management implications.

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Spatial and temporal patterns in the demersal fish community on the shelf and upper slope regions of the Gulf of Alaska

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The continental shelf and upper slope of the Gulf of Alaska (GOA, Fig. 1) support a diverse community of demersal fishes. This community includes many commercial species that support rich bottom trawl and longline fisheries with landings averaging approximately 250,000 metric tons per year over the past two decades (NPFMC[1]). The commercially most important species during the past decade have been walleye pollock (*Theragra chalcogramma*), Pacific halibut (*Hippoglossus stenolepis*), Pacific cod (*Gadus macrocephalus*), other flatfish species (Pleuronectidae), rockfish (*Sebastes* spp.), and sablefish (*Anoplopoma fimbria*). Arrowtooth flounder (*Atheresthes stomias*), although currently the dominant demersal species by biomass, is a minor component of total landings.

Triennial bottom trawl surveys have been carried out since 1984 to assess the abundance and distribution of the main commercial species in the GOA (Martin, 1997). The surveys also provide data on noncommercial fish species and other associated benthic megafauna. At least 140 species of fishes belonging to 33 families were collected during the 1996 GOA bottom trawl survey (Martin, 1997). Rockfish (Scorpaenidae) were the best represented family with 25 species, followed by sculpins (Cottidae, 24 species) and flatfishes (Pleuronectidae, 16 species). Data from similar bottom trawl surveys have been used to investigate the ecology and zoogeography of fish assemblages in many parts of the world, including the North Pacific (Gabriel and Tyler, 1980; Rogers and Pikitch, 1992; Jay, 1996). However, to our knowledge there have been no studies in which demersal fish assemblages from the GOA shelf and slope were examined.

To understand, and eventually to predict, the effects of environmental variations on fish stocks, scientists and managers increasingly advocate ecosystem approaches to research and management (Yaffee et al., 1996; Langton and Haedrich, 1997). Ecosystem management must be based on multispecies relationships and overcome the current focus on individual species (Langton and Haedrich, 1997). An important prerequisite for successful multispecies approaches is an understanding of the species structure of fish communities in space and time.

The purpose of this paper is to identify spatial and temporal patterns in the composition of the demersal fish community from the GOA. Specific objectives are 1) to identify the main environmental and spatial gradients along which the groundfish community is structured, and 2) to identify long-term changes in the composition of the groundfish community.

[1] NPFMC (North Pacific Fisheries Management Council). 1997. Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska. North Pacific Fisheries Management Council, 605 West 4th Ave., Suite 306, Anchorage, AK 99501.

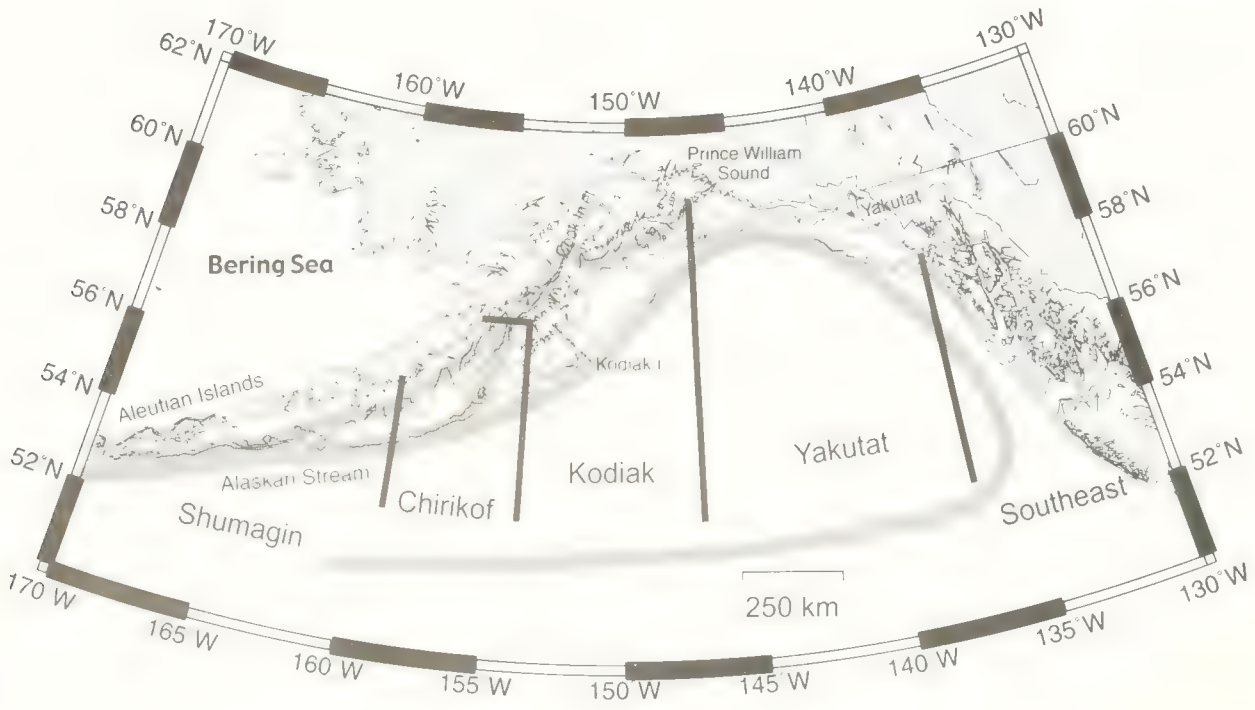

Figure 1

Bathymetric and geographic features of the Gulf of Alaska between 130°W and 170°W. The black vertical lines separate the five areas used in the survey design and analysis. Thin lines indicate 100 m, 200 m, and 500-m isobaths. The large shaded lines summarize major circulation patterns.

Materials and methods

Study area

Our study area included the continental shelf and the upper continental slope along the perimeter of the GOA to a depth of 500 m (Fig. 1). The total study area is approximately 300,000 km^2, extending over a distance of 2600 km from Southeast Alaska to the western Aleutian Islands.

Data sources

All fisheries data for this study were obtained from the Alaska Fisheries Science Center (AFSC), National Marine Fisheries Service (NMFS) in Seattle, WA. Personnel from AFSC have executed bottom trawl surveys of groundfish stocks in the GOA on a triennial basis since 1984 (Table 1). All surveys were conducted during the summer with chartered fishing vessels and were based on a stratified random sampling design. The GOA was divided into five areas, three in the western GOA (Shumagin, Chirikof, Kodiak) and two in the eastern GOA (Yakutat, Southeast, see Fig. 1) and four depth strata (0–100 m, 100–200 m, 200–300 m, 300–500 m). Depth strata within each area were further subdivided into 2–5 strata based on the type of geographical area (e.g. banks, gullies, shelf, and slope), resulting in a total of 49 strata. Some modifications were made to the stratification scheme after 1987. Our analysis was based on current stratum boundaries. Details of the sampling design, data collection, and sample processing are described in Brown (1986), Martin and Clausen (1995), Stark and Clausen (1995), and Martin (1997). In our analysis we excluded data from the 0–100 m stratum in the southeast area because it is mostly untrawlable and was not sampled during three out of five surveys; thus we used a total of 48 strata in the analysis. We further excluded all hauls that were classified as unsatisfactory in the database.

Several types of fishing gear were used in the bottom trawl surveys between 1984 and 1996. A poly-Nor'eastern high opening bottom trawl equipped with rubber bobbin roller gear has become the standard gear for GOA bottom trawl surveys (Munro and Hoff, 1995) and was used for at least part of the survey in all years (Table 1). In addition, an older Nor'eastern trawl (gear type 160) was used during parts of the 1984 and 1990 survey and two different Japanese trawls (Table 1) were used during the 1984 and 1987 joint Japanese-American surveys. Fishing effort for each gear type was spread out over most of the sampling region within each year and one gear type (gear type 172) was used during all surveys, allowing us to estimate gear differences.

Data analysis

Our analysis was based on standardized catch per unit of effort of 72 fish taxa collected in the bottom trawl surveys. Catches were standardized to weight per unit area (kg/km^2), where the area swept by the trawl was estimated

Table 1

Number of quantitative hauls used in analysis by gear type, start and ending dates of survey, minimum, maximum, and average depth of hauls, and number of haul locations for which bottom temperature was obtained. Note changes in gear from 1984 to 1990 which were associated with a decrease in the average tow duration. Gear types: 160 = Nor'eastern trawl; 172 = poly-Nor'eastern high opening bottom trawl; 710 = Japanese poly trawl; 717 = Japanese poly trawl with roller gear.

	1984	1987	1990	1993	1996
Total number of hauls	867	758	705	774	807
Gear type: no. of hauls	(160: 430) (172: 133) (710: 304)	(172: 380) (717: 378)	(160: 166) (172: 539)	(all: 172)	(all: 172)
Starting date	Jun 3	May 22	Jun 4	Jun 6	May 22
Ending date	Oct 2	Sep 10	Sep 9	Sep 7	Jul 30
Average depth (m)	167	150	167	156	157
Maximum depth (m)	499	499	494	488	479
Minimum depth (m)	16	20	20	22	20
Temp. measurements	563	298	285	726	716

from the measured distance trawled and estimates or measurements of the width of the net opening. Taxa to include in the analysis were selected according to the following criteria: 1) all species consistently identified to species level and occurring at least at 1% of the stations, 2) taxa that were not consistently identified to species level were combined by genus or, if necessary, by family, 3) if, after grouping taxa, a species, genus, or family was present at less than 1% of the stations within each year, it was not included in the analysis.

As an initial estimate of abundance trends, we computed gulf-wide averages of CPUE for each species by year. CPUEs from the Japanese trawls used in 1984 and 1987 were adjusted to the US standard trawl gear by using fishing power coefficients provided in Tables 28 and 31 in Munro and Hoff (1995). Following standard NMFS methods (Martin, 1997), we averaged estimated CPUEs by stratum, weighted the averages by stratum area, and combined them to obtain area-wide averages.

From a haul-by-taxon matrix of CPUE data, we computed univariate and multivariate indices to examine spatial and temporal patterns in community structure. For each haul we computed species richness (number of species), species diversity (Shannon-Wiener index), and total CPUE of all groundfish taxa combined as univariate measures of community structure. We considered three indices of species diversity (Shannon-Wiener, Simpson's D, Fisher's α) and chose the Shannon-Wiener index because it showed little dependence on sample size in simulations, was approximately normally distributed (which facilitates statistical comparisons), and is widely used in the ecological literature. In addition, we computed multivariate indices of species composition based on Bray-Curtis dissimilarities of root-root transformed CPUEs and nonmetric multidimensional scaling (NMDS) as described in Mueter and Norcross (1999). Indices of species composition were computed separately for each year and were related to explanatory variables to describe the major gradients in species composition by year. To examine trends in species composition over time, catches were averaged by stratum instead of using individual hauls, reducing the 3911 hauls to 240 within-year strata (5 years × 48 strata). An NMDS ordination of the stratum-by-species matrix was then used to test specifically for significant trends in species composition over time. We computed the linear combination of ordination axes that maximized the correlation with year and tested whether the correlation was significantly higher than would be expected by chance by using randomization tests. This linear combination was used as an index representing changes in species composition over time (time index). Species that were most strongly associated with the time index were identified based on scatterplots and Spearman rank correlations between the index and individual species abundances, and changes in these species were examined in more detail.

Depth, geographic location, bottom temperature (measured by sensors attached to the gear), Julian day, year, gear type, and area swept were included in the analysis as explanatory variables. Geographic location was represented in the analysis either as a categorical variable by using the five statistical areas depicted in Figure 1 or by using alongshore distances (AD). Alongshore distance was computed by projecting each station onto a line that approximately followed the shelf break and measuring the distance along this line from its origin in the southeast part of the study area (km 0) to the westernmost point (km 2600). Temperature was not measured for all hauls (Table 1); thus all regressions were done both with and without temperature included. Gear type was included in all models to account for potential differences among gear types. Area swept was only included for examining trends in species richness and diversity because the number of species per haul was expected to increase with the area sampled. All other indices were based on standardized CPUEs.

Generalized additive models (GAM, Hastie and Tibshirani, 1990) and linear models were used to relate univariate and multivariate indices, individual species CPUEs, and presence-absence data to the independent variables. Additive models were used to allow for nonlinear relationships between the dependent and independent variables. A GAM is a nonparametric regression that uses smooth functions of the independent variables in place of linear functions and allows different probability distributions for the data. We initially assumed that species richness followed a Poisson distribution (counts), that the Shannon-Wiener index, log-transformed CPUEs, and all indices of species composition followed a normal distribution, and that presence-absence data followed a binomial distribution. The dependent variables were then modeled as the sum of nonparametric functions (smoothing splines) of the hypothesized independent variables. If no evidence of nonlinearity was found, linear terms were substituted for the smoothing splines. Residuals from each regression model were examined for violations of the underlying assumptions (error distribution and homogeneity of variance) and for outliers. Specifically, we examined residuals graphically by means of histograms, quantile-quantile plots, and plots of residuals against time and against other covariates. We further conducted formal tests of goodness-of-fit of the residuals against the assumed error distributions after each model fit. Model fits were generally deemed adequate, unless noted otherwise in the results.

To identify and evaluate the significance of relationships between species composition and explanatory variables we first chose the most appropriate regression model, then quantified the contribution of each explanatory variable to the model fit. A stepwise procedure based on the Akaike information criterion (Hastie and Tibshirani, 1990) was used to select a subset of significant variables. As a measure of model fit we computed a pseudo-coefficient of determination (pseudo-r^2), or the fraction of the total deviance explained by the model, as a surrogate for the familiar r^2 (Swartzman et al., 1992). The importance of individual variables in the model fits was evaluated similarly by using a pseudo-coefficient of partial determination based on reduced models that exclude the variable of interest (= 1 – deviance of best model/deviance of reduced model).

Trends in the abundance of those species that were strongly associated with the time index were examined in greater detail by haul. For this analysis we treated zero and nonzero catches separately to test for 1) changes in the catch rate of a species over time based on positive catches only (CPUE-where-present) and 2) changes in the frequency of occurrence of a species over time (by estimating the probability of a nonzero haul). To test for changes in the CPUE-where-present of these species, we used an analysis of covariance model of the following form:

$$\log(CPUE\text{-}where\text{-}present) = area + depth\ stratum + gear + (area \times depth\ stratum) + \beta \times year.$$

Errors were assumed to be normally distributed, thus CPUE-where-present was assumed to follow a lognormal distribution. A separate linear time trend was estimated and evaluated for significance within each depth stratum in each area (β parameters). The interaction term (*area* × *depth stratum*) was omitted if it was not significant at the 5% level. Strata within the same statistical area and depth stratum were pooled, unless fitting separate regression lines to each of the 48 strata improved the overall fit significantly. If the slope of the regression did not differ among areas or depth strata at the 5% level, data were further pooled across areas or depth strata (or both) to obtain the most parsimonious model.

The probability of nonzero hauls was estimated similarly using a logistic regression model (McCullagh and Nelder, 1989):

$$\log\left(\frac{\Pr(CPUE>0)}{1-\Pr(CPUE>0)}\right) = area + depth\ stratum + gear + (area \times depth\ stratum) + \beta \times year,$$

where the number of positive catches (CPUE>0) was assumed to follow a binomial distribution. The most parsimonious models for each species were used to test the null hypothesis that there was no significant (linear) trend in the catch rate (CPUE-where-present) or frequency of occurrence (Pr{CPUE>0}) over time. The null hypothesis was rejected if the slope β was significantly different from zero at the 5% level.

Results

Arrowtooth flounder had the highest average CPUE (kg/km^2) and the highest frequency of occurrence during all surveys (Table 2). Walleye pollock was second in most years, followed by Pacific cod and Pacific halibut. However, in 1996, the estimated CPUE of Pacific Ocean perch exceeded that of pollock, cod, and halibut. Sablefish, five other flatfish species, two *Sebastes* species, and Atka mackerel (*Pleurogrammus monopterygius*) were other important species by CPUE (> 200 kg/km^2, Table 2). The most abundant species, including gadids and most of the flatfishes, were generally also the most widespread species in the survey (>50% frequency of occurrence). In spite of relatively high CPUEs, rockfishes, Atka mackerel, and yellowfin sole (*Limanda aspera*) had low frequencies of occurrence (4–40%), indicating high local abundances and a more restricted spatial distribution.

Independent variables used in the analysis of species richness, diversity, CPUE, and species composition were moderately correlated (Table 3). The largest correlations were between area swept and year (–0.452), due to a reduction in haul duration after 1987, between depth and temperature (–0.407), and between Julian day and alongshore distance (–0.383). Depth and bottom temperature on the shelf and slope are invariably confounded and their effects may generally be difficult to separate. The confounding between Julian day and AD was extreme in some years (e.g. r=–0.79 in 1993) because sampling vessels traveled from west to east during most surveys. However

Table 2

All groundfish taxa included in analysis and their estimated average CPUE (kg/km^2) by year and for all years combined. CPUEs were computed for each haul, averaged by stratum, weighted by stratum area, and combined to obtain area-wide averages. FO denotes overall frequency of occurrence for all years combined in percent.

Scientific name	Common name	1984	1987	1990	1993	1996	Mean	FO
Atheresthes stomias [1]	arrowtooth flounder	3790	3339	6499	5298	5574	4900	91
Theragra chalcogramma [1]	walleye pollock	2431	3139	2873	2586	2320	2670	74
Gadus macrocephalus [1]	Pacific cod	1876	1516	1424	1397	1821	1607	73
Hippoglossus stenolepis [1]	Pacific halibut	1415	1410	1118	2007	1936	1577	77
Sebastes alutus [1]	Pacific Ocean perch	753	823	535	1649	2629	1278	40
Anoplopoma fimbria [1]	sablefish	753	1379	731	844	492	840	52
Hippoglossoides elassodon [1]	flathead sole	912	783	828	643	689	771	57
Lepidopsetta spp. [1]	rock sole	515	668	531	590	695	600	44
Sebastes polyspinis [1]	northern rockfish	135	475	365	356	337	334	20
Pleurogrammus monopterygius	Atka mackerel	153	98	101	73	1179	321	5
Glyptocephalus zachirus [1]	rex sole	187	269	335	297	245	266	67
Microstomus pacificus [1]	Dover sole	164	263	329	291	266	263	55
Limanda aspera [1]	yellowfin sole	313	192	196	277	162	228	7
Sebastes ciliatus [1]	dusky rockfish	87	505	91	194	255	227	20
Sebastes aleutianus [1]	rougheye rockfish	153	227	165	212	156	183	34
Rajidae unident.	skate (unidentified)	139	129	164	205	274	182	33
Clupea pallasi	Pacific herring	186	511	60	53	3	163	8
Sebastes zacentrus	sharpchin rockfish	23	274	131	81	220	146	10
Albatrossia pectoralis	giant grenadier	115	96	81	155	175	124	3
Sebastolobus alascanus	shortspine thornyhead	126	127	68	114	177	122	24
Sebastes variegatus	harlequin rockfish	9	247	60	32	68	83	11
Thaleichthys pacificus	eulachon	24	56	95	119	110	81	32
Isopsetta isolepis [1]	butter sole	80	71	59	102	71	77	7
Platichthys stellatus [1]	starry flounder	50	63	35	137	93	76	5
Sebastes borealis	shortraker rockfish	59	137	43	69	69	75	8
Sebastes proriger	redstripe rockfish	18	90	92	101	51	71	4
Squalus acanthias	spiny dogfish	34	34	65	114	96	69	16
Hemilepidotus jordani	yellow Irish lord	49	46	40	40	61	47	27
Sebastes brevispinis	silvergray rockfish	16	18	48	65	82	46	7
Ophiodon elongatus	lingcod	15	32	35	53	80	43	10
Hemitripterus bolini	bigmouth sculpin	54	35	29	19	14	30	18
Lamna ditropis	salmon shark	27	43	42	26	11	30	1
Myoxocephalus spp.	sculpin (unidentified)	37	23	18	22	30	26	9
Parophrys vetulus [1]	English sole	11	28	26	28	15	22	7
Somniosus pacificus	Pacific sleeper shark	1	1	6	29	72	22	1
Zaprora silenus	prowfish	13	24	15	28	23	21	11
Pleuronectes quadrituberculatus [1]	Alaska plaice	7	16	20	9	17	14	4
Microgadus proximus	Pacific tomcod	5.03	34.67	6.32	9.01	5.78	12.16	2
Sebastes babcocki	redbanded rockfish	4.88	6.21	11.20	12.53	15.54	10.07	11
Hydrolagus colliei	spotted ratfish	13.06	8.16	6.32	7.08	12.65	9.45	6
Hexagrammos decagrammus	kelp greenling	3.89	8.17	13.87	8.21	6.69	8.16	8
Sebastes reedi	yellowmouth rockfish	1.69	0.89	6.39	12.14	3.15	4.85	1
Sebastes ruberrimus	yelloweye rockfish	2.10	10.17	3.29	3.88	3.70	4.63	3
Sebastes helvomaculatus	rosethorn rockfish	1.99	5.12	2.50	2.54	7.71	3.97	4
Sebastes melanops	black rockfish	1.14	3.75	4.65	0.86	7.89	3.66	1
Bathymaster signatus	searcher	2.08	2.05	5.39	3.04	4.38	3.39	15
Trichodon trichodon	Pacific sandfish	7.56	3.71	2.45	1.76	0.52	3.20	3
Malacocottus spp.	sculpin (unidentified)	4.33	2.97	2.40	3.55	1.63	2.97	14
Cryptacanthodes giganteus	giant wrymouth	0.76	3.26	3.98	1.17	2.77	2.39	1
Lycodes palearis	wattled eelpout	0.86	1.75	3.10	3.16	2.30	2.23	11

continued

Table 2 (continued)

Scientific name	Common name	1984	1987	1990	1993	1996	Mean	FO
Eopsetta jordani	petrale sole	0.97	0.83	0.61	2.77	3.68	1.77	2
Mallotus villosus	capelin	1.47	0.17	0.51	0.42	4.98	1.51	7
Lycodes brevipes	shortfin eelpout	0.13	0.84	0.79	2.41	2.17	1.27	8
Dasycottus setiger	spinyhead sculpin	1.33	0.49	0.89	1.88	0.83	1.08	11
Aptocyclus ventricosus	smooth lumpsucker	0.74	1.29	1.77	0.37	0.56	0.95	2
Podothecus acipenserinus	sturgeon poacher	0.19	0.42	1.23	2.34	0.33	0.90	5
Sebastes elongatus	greenstriped rockfish	0.05	0.22	0.59	0.91	1.20	0.59	1
Sebastes wilsoni	pygmy rockfish	0.00	1.38	0.30	0.01	0.96	0.53	1
Myctophidae	lanternfish (unidentified)	0.19	0.19	0.11	1.52	0.53	0.51	4
Triglops spp.	sculpin (unidentified)	0.37	0.32	0.68	0.40	0.61	0.48	6
Stichaeidae	prickleback (unidentified)	0.58	0.05	0.51	0.70	0.41	0.45	4
Sebastes crameri	darkblotched rockfish	0.02	0.13	0.59	0.99	0.41	0.43	1
Hexagrammos stelleri	whitespotted greenling	0.17	0.56	0.64	0.33	0.27	0.39	1
Lyopsetta exilis	slender sole	0.10	0.07	0.29	0.77	0.59	0.37	5
Cyclopteridae (Liparidinae)	snailfish	0.30	0.23	0.30	0.28	0.04	0.23	3
Hemilepidotus hemilepidotus	red Irish lord	0.07	0.29	0.05	0.32	0.10	0.16	1
Cottidae	sculpin (unidentified)	0.25	0.00	0.28	0.08	0.01	0.12	1
Gymnocanthus spp.	sculpin (unidentified)	0.16	0.03	0.00	0.06	0.06	0.06	1
Eumicrotremus orbis	Pacific spiny lumpsucker	0.02	0.08	0.03	0.07	0.04	0.05	2
Lycodes diapterus	black eelpout	0.08	0.05	0.00	0.01	0.02	0.03	2
Sarritor frenatus	sawback poacher	0.03	0.03	0.01	0.04	0.04	0.03	2
Bathyagonus nigripinnis	blackfin poacher	0.02	0.01	0.01	0.01	0.00	0.01	1
Total		14,786	17,286	17,436	18,400	20,662	17,714	

Catches for 1984 and 1987 were adjusted by using fishing power coefficients in Tables 28 and 31 in Munro and Hoff (1995). Other flatfishes were adjusted by using rock sole coefficients.

Table 3

Pairwise Pearson's correlation coefficients among independent variables used in the statistical analysis.

	Depth	Alongshore distance	Gear temperature	Julian day	Year
Alongshore distance	–0.326*				
Gear temperature	–0.407*	–0.203*			
Julian day	0.129*	–.383*	0.330*		
Year	–0.026	–0.035	–0.266*	–0.306*	
Area swept	0.012	0.184*	0.019	0.145*	–0.452*

* Highly significant (P<0.01).

the direction of sampling was reversed in some years, providing some contrast.

Species richness, as measured by the number of species per haul, was initially modeled as a Poisson variable (counts). However, an analysis of the distribution of the observed numbers and of residuals from the fitted models suggested that it could more appropriately be modeled as a normally distributed variable (see below). We fitted models assuming either a Poisson or a normal distribution and found that the estimated patterns were virtually identical and in both cases the same model was selected as best model. Only results based on the normal distribution are presented. Species richness was highly variable and the best model explained a small portion of the overall variability (Pseudo-r^2=0.25). The average number of species increased with area swept (Fig. 2), which may be expected if species area relationships established for terrestrial ecosystems also hold in the marine environment. The number of species tended to peak at intermediate depths (200–300 m) and was highest in the eastern GOA (Table 4), decreasing steadily west of Prince William Sound (km 1100, approximately 147°W). Species richness appeared

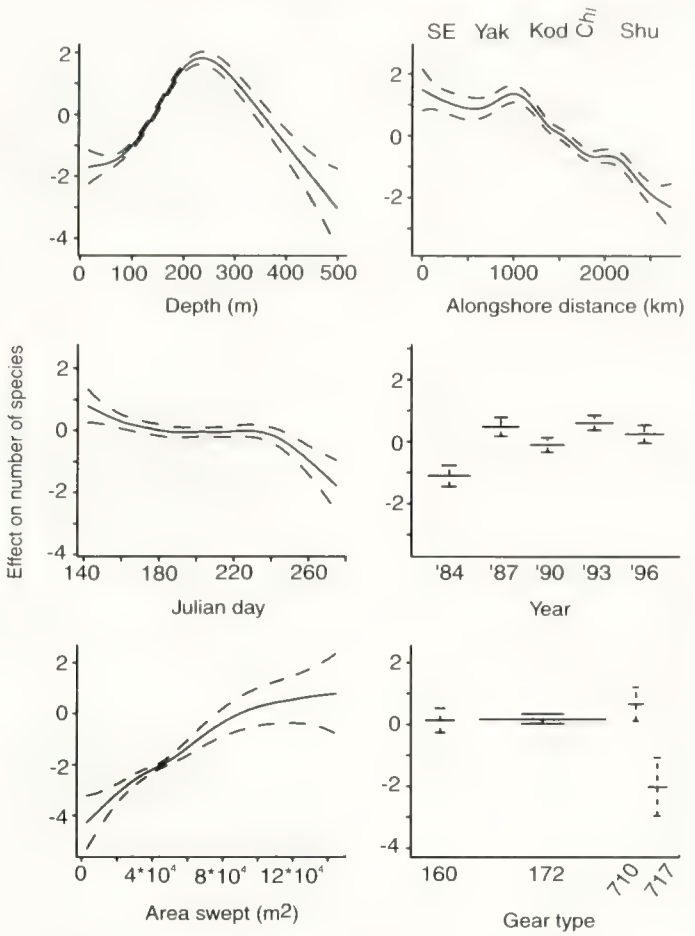

Figure 2

Estimated trends in number of species per haul by depth, alongshore distance, Julian day, year, area swept, and gear type. Alongshore distance was measured along the 200-m depth contour from east to west. Major geographic regions from east to west are Southeast (SE), Yakutat (Yak), Kodiak (Kod), Chirikof (Chi), and Shumagin (Shu). Dashed lines indicate approximate 95% confidence limits of the regression lines. Horizontal lines in lower right plots indicate mean response with 95% pointwise confidence intervals. Width of bars is proportional to number of observations. Fitted lines in each panel are adjusted for the effects of all other variables. Standardized effects in each plot (y-axes, no units) are on the same scale for comparison. Effects are standardized because the estimated CPUE at a given value of a variable is dependent upon the levels of all other variables.

to decrease during the last month of the survey season and showed some variation across years (Fig. 2). There was no consistent trend in species richness with temperature (not shown). One of the Japanese trawls (gear type 717, Fig. 2) tended to have a much smaller number of species per haul on average, suggesting a low catchability for at least some species. Residuals from the best model were close to normally distributed (Fig. 3, A and B) and showed no apparent trends with any of the covariates or over time.

Only a very small portion of the variability in species diversity (Shannon-Wiener index) was accounted for by the best regression (Pseudo-r^2=0.17). Depth had the strongest effect on species diversity with highest diversities observed at intermediate depths (Fig. 4). Diversity generally increased with the number of species, which showed a very similar trend with depth (Fig. 2). Diversity was higher in the eastern Gulf and decreased west of Prince William Sound (Figs. 4 and 5). It showed little variation over time, both within the survey period and across years. However,

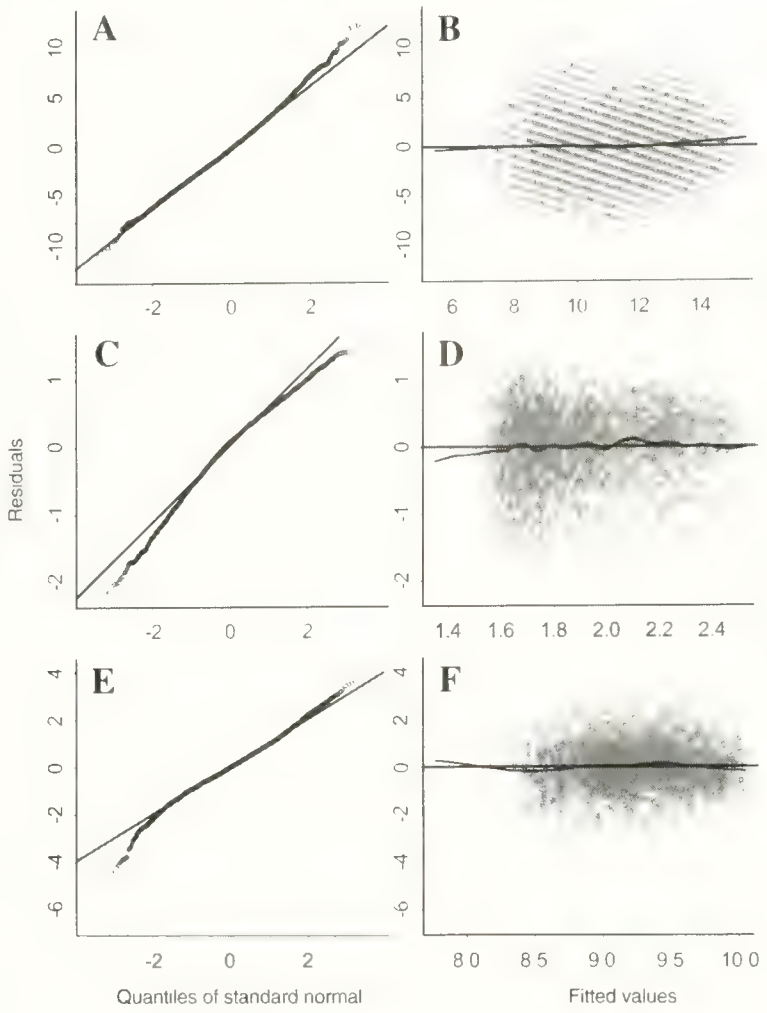

Figure 3

Quantile-quantile plots (left), showing sorted residuals (points) against corresponding quantiles of the standard normal distribution, and plots of residuals against fitted values with smoothing spline (right) for best-fit models of species richness (**A**, **B**), species diversity (**C**, **D**), and total CPUE (**E**, **F**). Points in Q-Q plots fall on the indicated straight line if data are normally distributed.

Table 4

Average number of groundfish species caught per haul by depth stratum and geographic area, not adjusted for effects of other variables.

Depth stratum (m)	No. of species/haul (SE)	Area	No. of species /haul (SE)
0–100	9.5 (0.12)	Shumagin	9.7 (0.11)
100–200	11.5 (0.08)	Chirikof	10.5 (0.12)
200–300	13.2 (0.13)	Kodiak	11.6 (0.11)
300–500	10.9 (0.15)	Yakutat	12.5 (0.14)
		Southeast	12.8 (0.20)

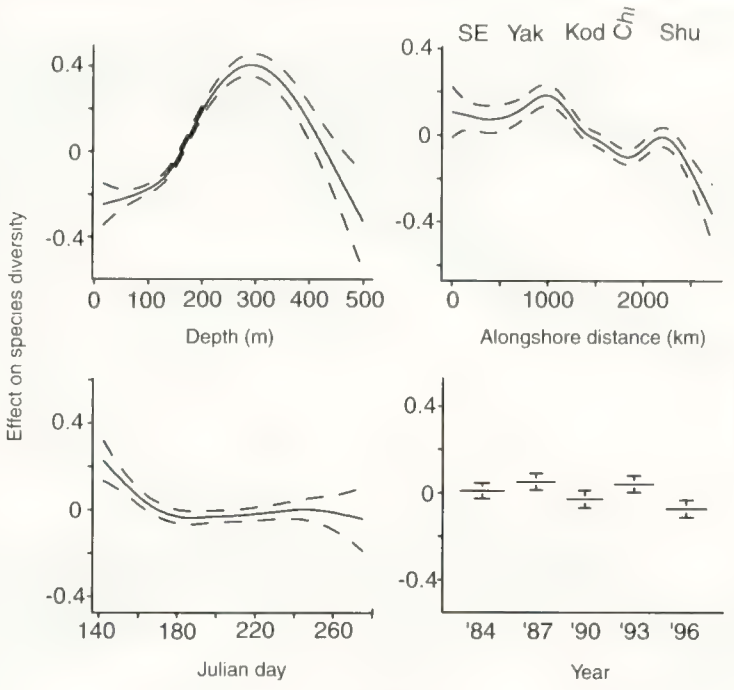

Figure 4

Trends in species diversity (Shannon-Wiener index) by depth, alongshore distance, Julian day, and year (area swept and gear type were not significant). For details see Figure 2.

95% confidence intervals suggest a significant drop in species diversity between 1993 and 1996. Area swept and temperature did not enter the best model, suggesting they had no strong effect on species diversity. Diagnostic plots indicated approximate normality and no apparent trends in the residuals (Fig. 3, C and D).

Total biomass (CPUE) showed strong trends with depth and alongshore distance (Fig. 6) but had high variability around these trends (Pseudo-r^2=0.14). Average CPUE increased sharply with depth to about 150 m—a trend that reflected, on average, approximately a doubling of CPUE between the shallowest sampling stations and stations at 150–200 m depth. A similarly strong gradient exists in the alongshore direction between Yakutat (km 700) and the Kodiak Island area (km 1500), where total CPUE has a pronounced maximum. Estimates of the spatial trend suggested that highest CPUEs are found around Kodiak Island, particularly in Shelikof Strait, along the shelf break and upper slope, and on the banks and in the gullies northeast of Kodiak Island (Fig. 5). Total CPUE appeared to decrease significantly after approximately Julian day 240 (Aug. 28); however, Julian day was confounded with alongshore distance (r =–0.38, Table 3) and the effect could in part be due to lower abundance in the eastern GOA, which was often sampled later than other areas. Gear effects were significant and indicated a lower catch rate for one of the Japanese trawls (gear 717, Fig. 6). The estimated time trend (Fig. 6) indicated a significant increase in total CPUE between 1984 and 1996 (P<0.001), based on a chi-square test of the difference in residual deviances (Hastie and Tibshirani, 1990). We estimated that the combined CPUE of all groundfish species included in the analysis increased from a gulf-wide average of 14,786 kg/km^2 in 1984 to 20,600 kg/km^2 in 1996 (Table 2), representing an increase of 40%. No significant effect of temperature on total CPUE was found. Diagnostic plots indicated approximate normality and no apparent trends in the residuals (Fig. 3, E and F).

The biomass of 72 groundfish species in 240 stratum/year combinations could effectively be summarized by an NMDS ordination in three dimensions (stress=0.085). Our findings suggested that the main gradients along which species composition varied were depth and alongshore distance, whereas temperature and temporal gradients (within and between years) had relatively minor effects on these indices of species composition. The first two dimensions (axes 1 and 2) of the ordination accounted for 67% and 19% of the overall variation respectively. An ordination plot of the first two axes indicated that the sample strata were most clearly separated along the depth gradient (Fig. 7). The alongshore gradient was roughly perpendicular to the depth gradient and clearly distinguished areas Southeast from the other areas (Fig. 7). Yakutat strata occupy an intermediate position between the Southeast strata and strata in other areas. Kodiak, Chiniak, and Shumagin were similar in species composition, as sug-

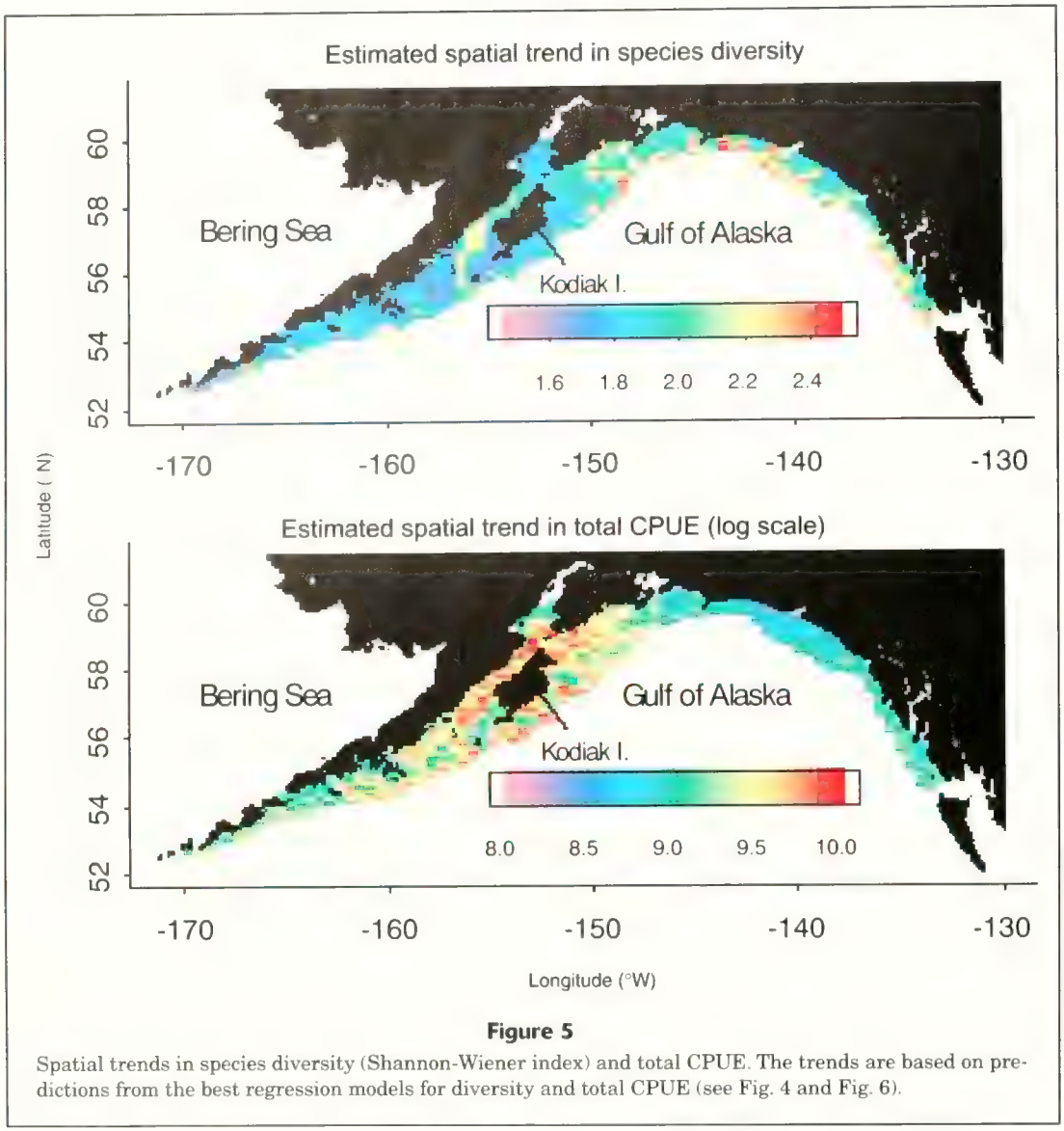

Figure 5

Spatial trends in species diversity (Shannon-Wiener index) and total CPUE. The trends are based on predictions from the best regression models for diversity and total CPUE (see Fig. 4 and Fig. 6).

gested by a substantial overlap in the location of strata in the ordination diagram. A three-way analysis of variance for each of the three axes by depth stratum, area, and year indicated highly significant differences for all three axes between depth strata and geographic areas, but weak and nonsignificant differences among years (Table 5), suggesting a relatively stable species composition from 1984 to 1996. Residuals from the ANOVA for axis 1 and 3 were approximately normally distributed and showed no apparent violations of the ANOVA assumptions. Residuals for axis 2 had a very long-tailed distribution, but an analysis of variance based on ranks yielded very similar results; therefore the conclusions appear to be robust.

Ordinations of individual hauls within each year confirmed that depth and alongshore distance explained much of the variation in species composition within years. The species composition in each year was effectively summarized by ordinations in five dimensions with Kruskal's stress values that were very close to 0.1 in all years (axes 1–5 in Table 6). The first axis of all five ordinations accounted for 42–47% of the variation in species composition. This axis, as well as most of the other axes, was most strongly related to the depth gradient in all years (Table 6). Alongshore distance appeared to explain a relatively small proportion of the variance in species composition. However the pseudo-coefficients of partial determination for alongshore distance typically increased substantially if Julian day was excluded from the model because of high correlations between Julian day and alongshore distances. Regressions of the axes on depth and alongshore distance alone resulted in pseudo-r^2 values that were very close to those from models that included Julian day. Furthermore, residuals from these models were not significantly related to Julian day for any year ($P>0.5$) based on linear regres-

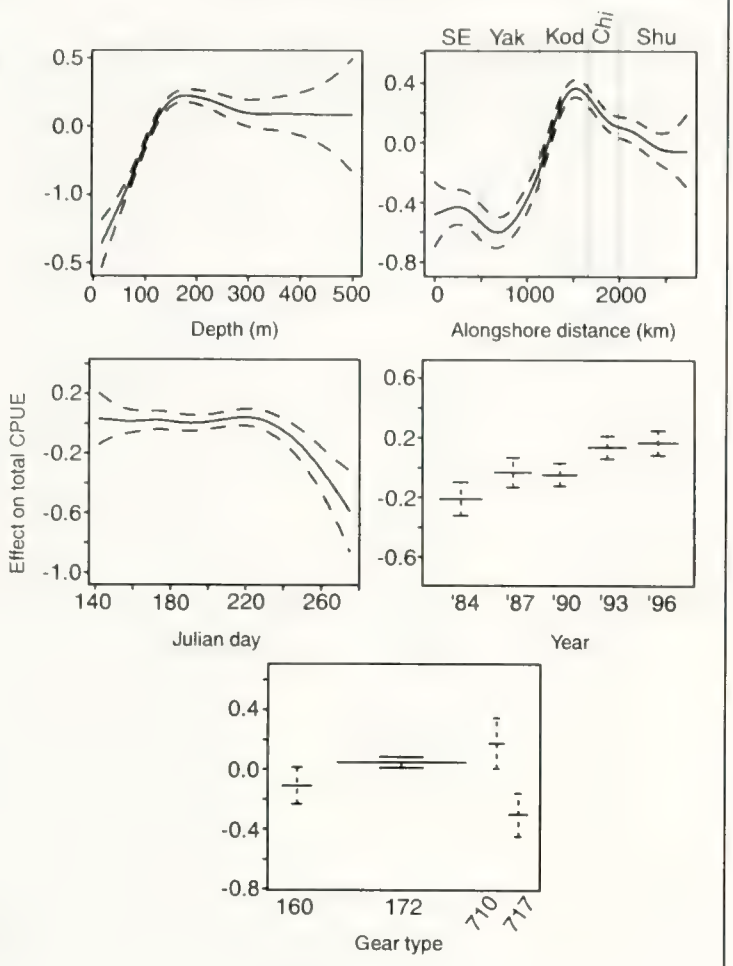

Figure 6

Trends in total CPUE by depth, alongshore distance, Julian day, year, and gear type. For details see Figure 2

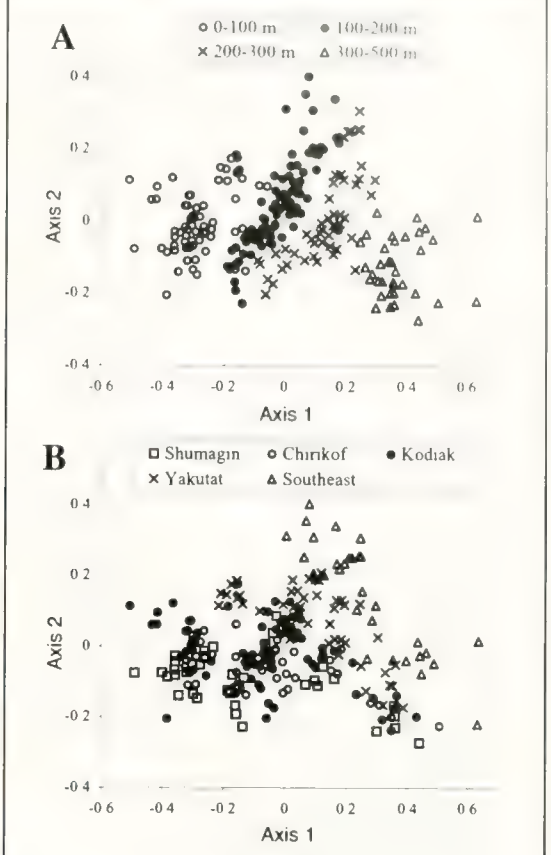

Figure 7

Plots of the first two axes from an NMDS (multidimensional scaling) ordination of 48 strata sampled during each of fivfe years. Distances between two points (strata) in the ordination diagram approximately reflect their dissimilarity in terms of species composition. Symbols indicate depth strata (**A**) and geographic area (**B**).

sions). These findings suggest that species composition within the summer remains relatively stable over the 14–16 week survey period.

To examine effects of temperature on species composition we used only those hauls from the 1993 and 1996 data for which temperature measurements were available (n=726 and n=716 respectively, Table 1). Results for other years are not reported because of the relatively small number of temperature measurements. The available temperature data for earlier years were often localized in certain strata, whereas large areas had few if any measurements. The lack of contrast did not allow definite conclusions with regards to the temperature effect. For 1993 and 1996, we repeated the GAM analysis for the five axes of species composition with temperature included. Temperature effects were apparently large. However, wide confidence intervals and inconsistent patterns between years suggest that the apparent effects were at least in part due to confounding of temperature with alongshore distance and depth. Therefore we first adjusted for the effects of depth and alongshore distance using the regression models summarized in Table 6. Temperature explained a small but significant portion of the remaining residual variation in three of the ordination axes in both 1993 and 1996 (Pseudo-r^2 values <0.1).

To identify which species were most strongly related to the major gradients we computed rank correlations between each species and the three axes of species composition based on the NMDS ordination of strata averages. We considered all species that had a positive or negative rank correlation of at least 0.4 with one of the axes for further examination, based on a visual inspection of scatterplots. Species associated with the first two axes were clearly separated along gradients of depth and alongshore distance (Figs. 8 and 9). The first axis was positively correlated with a number of deep-water species that were

Table 5

Analysis of variance of three axes of species composition by statistical area, depth stratum, and year.

Effect	df	Sum of squares	Mean squares	*F*-value	*P*-value
Axis 1					
Depth stratum	3	129.793	43.264	613.856	0.000
Area	4	10.350	2.588	36.713	0.000
Year	4	0.665	0.166	2.358	0.056
Depth stratum:area	11	1.756	0.160	2.265	0.014
Depth stratum:year	12	0.412	0.034	0.487	0.920
Area:year	16	0.291	0.018	0.258	0.998
Depth stratum:area:year	44	0.839	0.019	0.271	1.000
Residuals	145	10.220	0.070		
Axis 2					
Depth stratum	3	6.601	2.200	37.581	0.000
Area	4	27.771	6.943	118.587	0.000
Year	4	0.346	0.087	1.478	0.212
Depth stratum:area	11	1.091	0.099	1.694	0.080
Depth stratum:year	12	0.366	0.030	0.521	0.899
Area:year	16	1.017	0.064	1.086	0.374
Depth stratum:area:year	44	0.815	0.019	0.317	1.000
Residuals	145	8.489	0.059		
Axis 3					
Depth stratum	3	0.478	0.159	1.231	0.301
Area	4	9.541	2.385	18.423	0.000
Year	4	0.615	0.154	1.188	0.318
Depth stratum:area	11	3.080	0.280	2.163	0.019
Depth stratum:year	12	0.212	0.018	0.137	1.000
Area:year	16	0.698	0.044	0.337	0.992
Depth stratum:area:year	44	1.365	0.031	0.240	1.000
Residuals	145	18.773	0.129		

more abundant in the eastern GOA, but generally had a broad geographic distribution. The deep-water species included several rockfish species, rex sole (*Glyptocephalus zachirus*), Dover sole (*Microstomus pacificus*), sablefish, and myctophids. The alongshore distribution of CPUE suggests that many species displayed local maxima in biomass on the scale of 100–200 km (Fig. 8). The first axis was negatively correlated with a group of shallow-water species that were typically more abundant in the western GOA. The shallow-water group included a number of flatfish species, gadids, and sculpins. Many of the shallow water species had pronounced peaks in biomass at the longitude of Kodiak Island (km 1400–1700) and between the Shumagin Islands and Sanak Island (km 2000–2200).

The second axis was positively correlated with a "shelf break" group. Most of the species in this group had a pronounced peak in biomass near 200 m and were found primarily in the eastern GOA (Fig. 9). The group included a number of rockfish species, as well as lingcod (*Ophiodon elongatus*), petrale sole (*Eopsetta jordani*), and slender sole (*Lyopsetta exilis*). Species that were negatively or positively associated with the third axis (not shown) were not differentiated along gradients of depth and alongshore distance, suggesting that the third axis, which accounted for 14% of the overall variation, was related to other, unidentified gradients.

Finally, we examined trends in species composition over the 12-year period from the first survey in 1984 to the most recent survey in 1996 in more detail based on the NMDS ordination of species CPUEs averaged by stratum (Fig. 7). Although the individual indices of species composition were not significantly different among years (Table 5), a canonical correlation between the ordination axes and time (survey years) indicated a highly significant trend ($P<0.001$) in species composition. The linear combination of ordination axes that maximized the correlation with survey year was used as an index for the trend in species composition ("time index"). The index increased in most areas and depth strata between 1984 and 1996. Eight species that were positively correlated with the time index showed significant and increasing trends in either CPUE-where-present or frequency of occurrence for at least two area-depth stratum combinations (Fig. 10). Skates were most strongly associated with the index and showed a widespread increase in CPUE-where-present and frequency of occurrence, particularly in the Chirikof,

Table 6

Results from NMDS (multidimensional scaling) ordinations of species CPUEs in five dimensions (axes 1–5) by year, and GAM (generalized additive models) results for regressions of axis scores on depth, alongshore distance, and Julian day. Variance indicates proportion of overall variation accounted for by each axis. Stress indicates Kruskal's stress values for each ordination. Numbers for the full model indicate pseudo-r^2 values for the best model fit (1 – deviance of the best fitting model/deviance of the null model). Numbers following individual variables indicate pseudo-coefficient of partial determination, computed from a reduced model that excluded the variable (= 1 – deviance of best model / deviance of reduced model). Only coefficients of determination exceeding 0.1 are shown. Coefficient of determination for Julian day did not exceed 0.1 in any year or for any axis. AD = alongshore distances.

Year		Axis 1	Axis 2	Axis 3	Axis 4	Axis 5	Stress
1984	Variance	44%	19%	14%	12%	11%	0.102
	Full model	0.84	0.28	0.26	0.58	0.13	
	Depth	0.74		0.19	0.42		
	AD	0.12	0.13		0.12		
1987	Variance	42%	22%	14%	12%	10%	0.100
	Full model	0.77	0.22	0.32	0.36	0.21	
	Depth	0.67	0.11	0.28	0.19	0.17	
	AD	0.15			0.24		
1990	Variance	42%	21%	15%	12%	10%	0.096
	Full model	0.83	0.37	0.29	0.34	0.16	
	Depth	0.69	0.23	0.17	0.27	0.10	
	AD	0.11	0.12	0.17			
1993	Variance	47%	18%	13%	11%	11%	0.098
	Full model	0.81	0.24	0.37	0.49	0.31	
	Depth	0.71		0.26	0.42	0.27	
	AD				0.21		
1996	Variance	44%	20%	14%	12%	10%	0.099
	Full model	0.78	0.22	0.31	0.55	0.34	
	Depth	0.71	0.11	0.18	0.40	0.17	

Kodiak, and Yakutat areas (Figs. 10 and 11). Another elasmobranch (Pacific sleeper shark, *Somniosus pacificus*), two osmerids (capelin, *Mallotus villosus*, and eulachon, *Thaleichthys pacificus*), three flatfish species (Dover sole, rex sole, and arrowtooth flounder), and one rockfish species (Pacific Ocean perch, *Sebastes alutus*) increased significantly in one or more areas and depth strata (Fig. 10). The frequency of occurrence of capelin in the trawl survey increased significantly, whereas CPUE-where-present did not change or, in some cases, decreased significantly. Closer examination revealed that the increase in frequency of occurrence occurred primarily between 1993 and 1996 (Fig. 12). Capelin were caught in 14% of all hauls in 1996, compared to only 7% in 1993. Changes in the CPUE-where-present of three flatfish species differed among species. Although Dover sole increased primarily in the eastern GOA (Yakutat and Southeast), rex sole increased most strongly in the Chirikof area (Fig. 10). In contrast, arrowtooth flounder increased in all areas, but only in the 0–100 m depth stratum. Although all three flatfish species increased significantly over time, estimates of their gulf-wide average CPUEs were highest in 1990 and declined from 1990 to 1996 (Table 2). Both the frequency of occurrence and CPUE-where-present of Pacific Ocean perch increased strongly in the Chirikof area, and frequency of occurrence decreased in the Yakutat area.

CPUE-where-present of the four species that were negatively correlated with the time index did not decrease significantly, and, in the case of rock sole (*Lepidopsetta* spp.), even increased in some areas (Fig. 13). However, frequency of occurrence decreased significantly for three of the species, particularly for bigmouth sculpin (*Hemitripterus bolini*, Fig. 13).

Discussion

Research survey data provide standardized indices of relative abundance that often track abundance trends more accurately than methods that use commercial catch data (Pennington and Stromme, 1998). However, results need to be interpreted with caution because the catchability of species may change over time owing to changes in survey gear, vessel type, spatial distribution, or the length composition of a population. In our study we were particularly concerned that differences in gear type (Table 1) might bias our results. We opted to include gear type directly into the analysis as a "nuisance" variable, instead

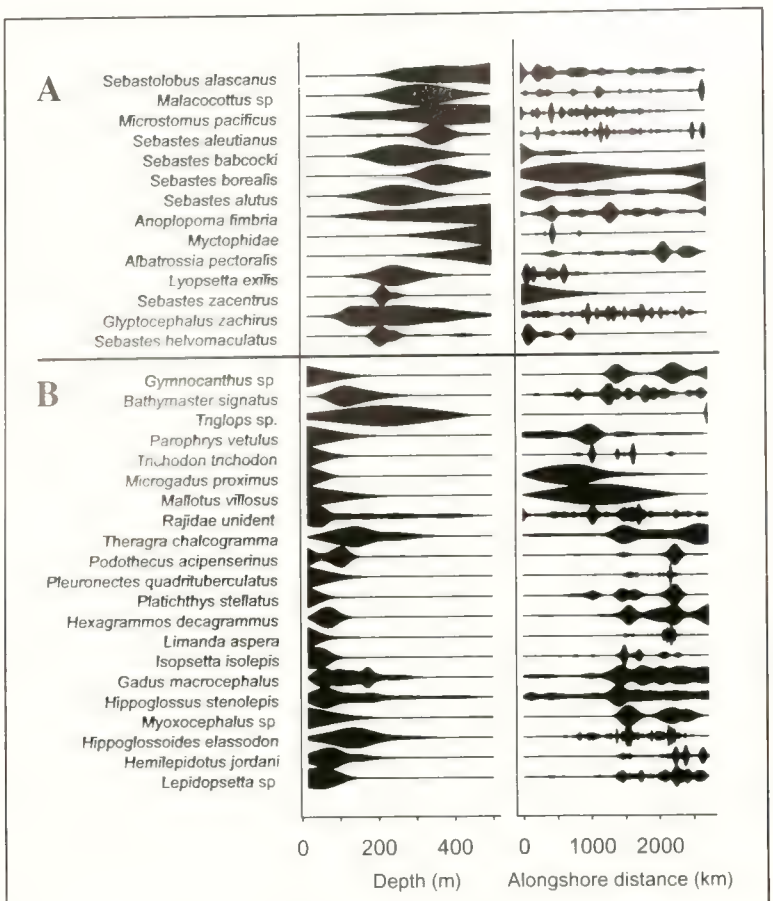

Figure 8

Distribution of CPUE by depth and alongshore distance for all species that had a strong positive (**A**) or negative (**B**) association with the first index of species composition derived from an NMDS ordination of abundances averaged by strata. Widths of dark bands are proportional to average CPUE of a given species. Average CPUE as a function of depth and alongshore distance was estimated by using a scatterplot smoother (cubic smoothing spline). Degree of smoothing was determined by cross-validation for each species separately.

of standardizing the CPUE of each species to a common gear standard prior to analysis because of large uncertainties in the estimation of fishing power coefficients (Munro and Hoff, 1995). The estimated differences among gear types agreed qualitatively with results in Munro and Hoff (1995) for those species for which these authors estimated fishing power. Nevertheless, differences among gear types may have biased some of our results. In spite of these problems, the survey data used in our study provided the best available indicator of relative changes in species composition and distribution for many species of ecological or commercial interest.

The observed trends in species richness, diversity, and biomass, as well as in the CPUE of individual species, showed that depth is an important gradient structuring the groundfish community in the GOA, and that the shelf break and upper slope (at 150–300 m) is a particularly important depth range. Strong depth-dependent gradients are found in many other demersal fish communities inhabiting shelf and upper slope regions (Colvocoresses and Musick, 1984; Gomes et al., 1992; Blaber et al., 1994; Fujita et al., 1995; Jay, 1996; Farina et al., 1997; Mahon et al., 1998). Distinct depth preferences of many individual species (Fig. 8) result in a turnover of species along the depth gradient and lead to the observed patterns in richness, diversity, and biomass. Similar to the altitude gradient in terrestrial environments (Brown and Lomolino, 1998), depth appears to be the major ecological gradient structuring benthic communities in the ocean from shallow, nearshore areas (Mueter and Norcross, 1999) to the abyssal plain (Merrett, 1992).

Our results suggest a pronounced peak in species richness, diversity, and total biomass at intermediate depths. Species richness as well as biomass of demersal fish com-

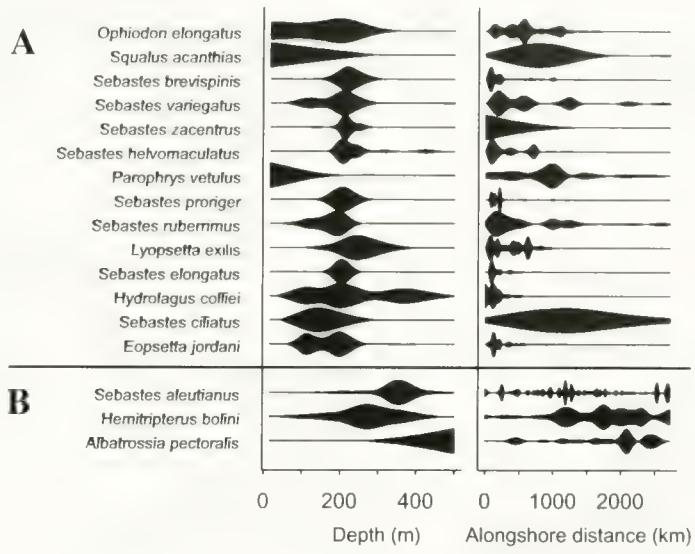

Figure 9

Distribution of CPUE by depth and alongshore distance for all species that had a strong positive (**A**) or negative (**B**) association with the second index of species composition derived from an NMDS ordination of abundances averaged by strata. For details see Figure 8.

munities are generally higher on the continental shelf than on adjacent slope regions, reflecting a strong gradient with depth (Day and Pearcy, 1968; Colvocoresses and Musick, 1984; Farina et al., 1997). In contrast to our results for the GOA, these studies did not find peaks in richness or biomass at intermediate depths. This may have been partly the result of aggregating data into relatively large depth ranges in those studies (and the associated loss in resolution), whereas our study examined patterns in richness and biomass along a continuous depth gradient.

We suggest that the high biomass of demersal fishes near the shelf break (in particular the biomass of flatfishes, rockfishes, and gadids) reflects favorable feeding conditions at this depth range. Favorable feeding conditions may result from enhanced benthic productivity or availability of suitable prey at this depth. The region along the shelf break and over the upper slope has high primary productivity that may be driven by shelf-break fronts, seasonal upwelling, strong alongshore currents, and tidal mixing (Parsons, 1986). Shelf-break fronts have frequently been observed in the GOA (Weingartner[2]) and can enhance phytoplankton and zooplankton biomass, particularly when coupled with upwelling (Mann and Lazier, 1991), which is common during the summer in the western GOA (Reed and Schumacher, 1986). We speculate that increased production in the water column becomes available to the benthos when sinking particles are consumed by larger organisms such as shrimp or euphausiids, which are often concentrated near the shelf break and are consumed by demersal fish (Mackas et al., 1997; Robinson and Gomez-Gutierrez, 1998). The most abundant demersal fishes in the GOA, arrowtooth flounder and walleye pollock, as well as several rockfish species, have been shown to feed near or off the bottom on euphausiids, mysids, copepods, shrimps, and other fishes (Yang, 1993). Thus, a region of enhanced benthic productivity near the shelf break is consistent with the total biomass of groundfish being highest just inshore of the shelf break between 150 and 200 m (Fig. 6).

In addition to depth (or elevation), latitude is a major ecological gradient in both marine and terrestrial environments. Demersal fishes on the continental shelf off both the east coast of North America (Mahon et al., 1998) and the U.S. west coast (Jay, 1996) form loose assemblages that are clearly separated by latitude. Although the latitudinal extent of our study region is relatively small, we found strong alongshore (roughly corresponding to longitudinal) differences in community structure from the eastern GOA to the Aleutian Islands, with the steepest gradient between the Yakutat and Kodiak areas. This gradient was apparent in species richness and diversity (Figs. 2 and 4), total CPUE (Fig. 6), and indices of species composition (Fig. 7). The alongshore gradient is perpendicular to the depth gradient, with depth generally increasing in the offshore direction. However, these two variables were moderately correlated (–0.32, ranging from –0.20 to –0.44 in individual years), primarily due to the larger number of shallow stations in the western part of the study area and a relative lack of shallow stations in Southeast Alaska.

[2] Weingartner, T. J. 2000. Personal commun. Institute of Marine Sciences, University of Alaska Fairbanks, Fairbanks, Alaska 99775.

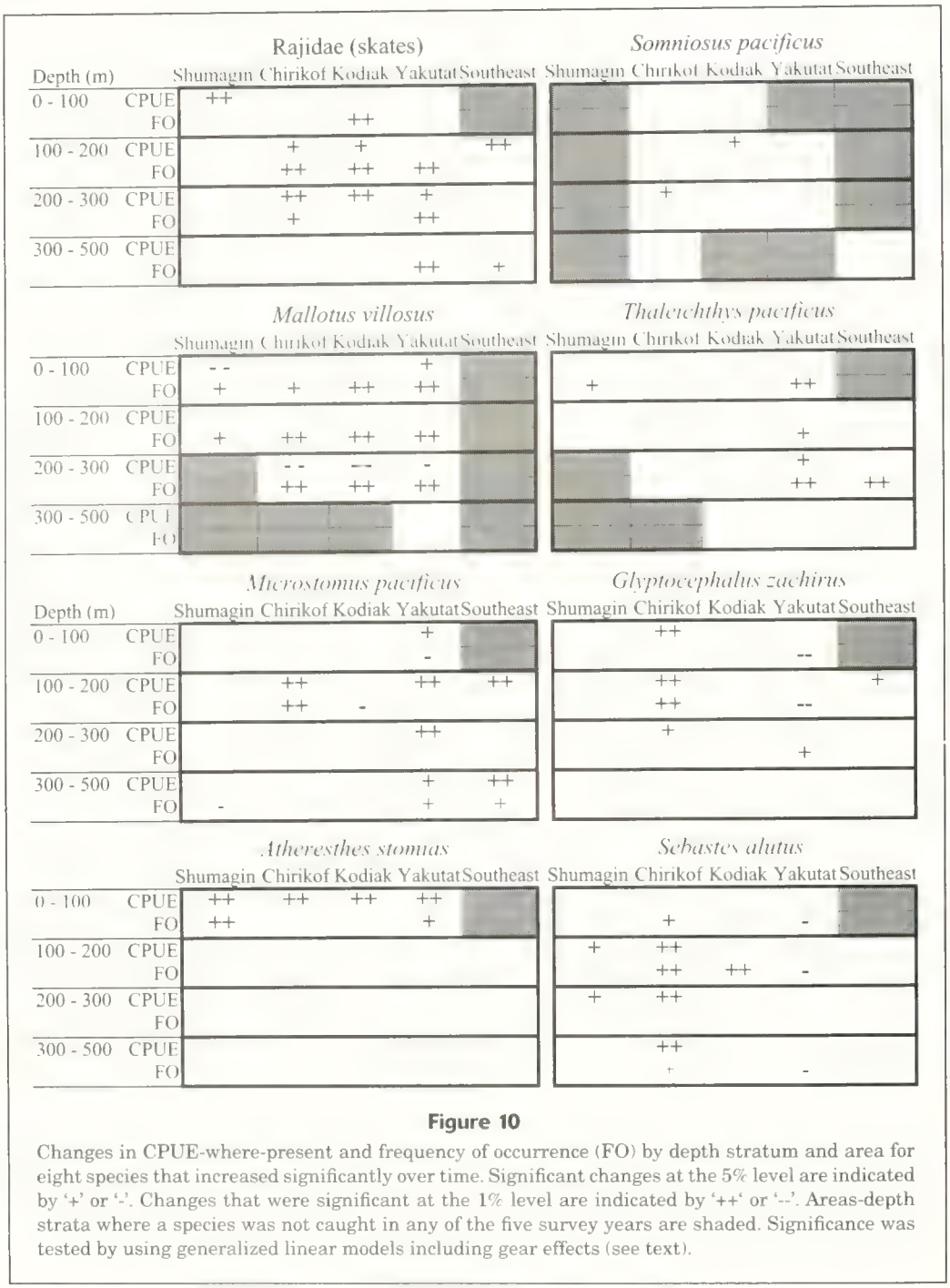

Figure 10

Changes in CPUE-where-present and frequency of occurrence (FO) by depth stratum and area for eight species that increased significantly over time. Significant changes at the 5% level are indicated by '+' or '-'. Changes that were significant at the 1% level are indicated by '++' or '--'. Areas-depth strata where a species was not caught in any of the five survey years are shaded. Significance was tested by using generalized linear models including gear effects (see text).

Therefore, the alongshore trends may be partly due to differences in the distribution of sampling depth between the eastern and western GOA resulting from differences in topography. Nevertheless, we do not believe that the magnitude of correlations (Table 3) presents a serious problem for the general patterns that were observed for CPUE, diversity, and species composition.

Alongshore patterns in CPUE (Figs. 5 and 6) indicate a higher biomass of demersal fishes in the western GOA, particularly in the Kodiak Island area. If the higher biomass is related to the availability of food, this pattern may reflect higher benthic productivity in the Kodiak Island region. There are several pieces of evidence that suggest a higher productivity in this region. First, there is a higher benthic biomass and productivity of infaunal organisms on the Chirikof and Kodiak shelf, compared with the Yakutat and Southeast areas (Semenov, 1965, as cited in Feder and Jewett, 1986). Second, enhanced primary productivity in the western GOA is evident in estimates from coastsl zone color scanner (CZCS) data and from more

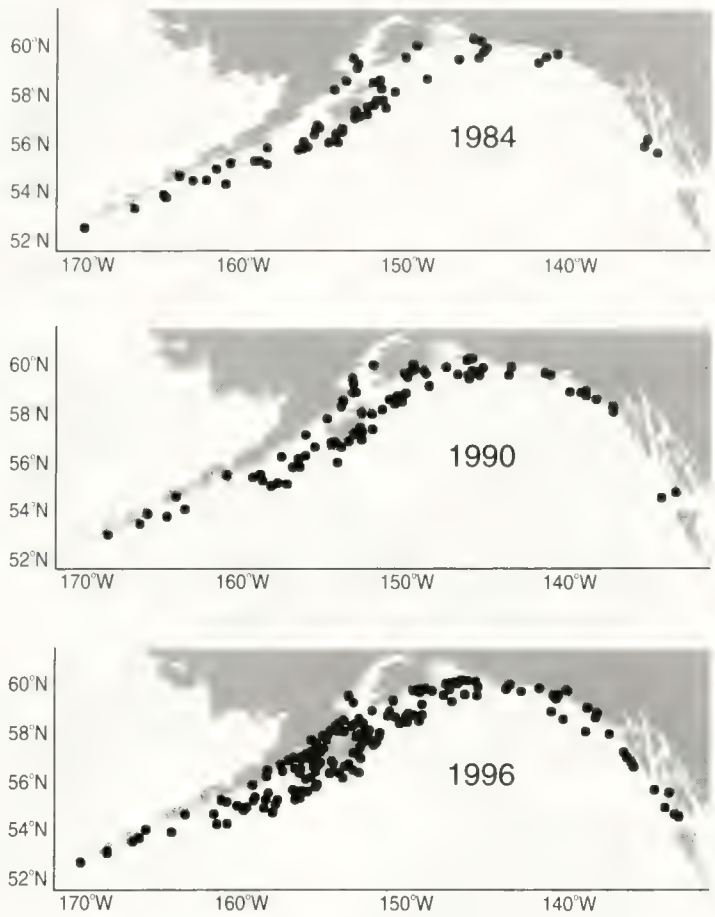

Figure 11

All sampling locations (•) where CPUE of skates (Rajidae) exceeded 300 kg/km^2 in 1984, 1990, and 1996.

recent SeaWifs data (Falkowski et al., 1998, see web site: http://seawifs.gsfc.nasa.gov/SEAWIFS.html). Third, the east–west gradient in productivity and biomass is consistent with differences in upwelling, which is generally more pronounced and more frequent in the western GOA (Reed and Schumacher, 1986). Fourth, the presence of strong tidal currents in the vicinity of Kodiak Island (Kowalik[3]) (see also Isaji and Spaulding, 1987) may further enhance demersal productivity (Mann and Lazier, 1991). Fifth, strong alongshore currents, advection, and nutrient input from major rivers may contribute to a higher productivity in the western GOA and around Kodiak Island. Finally, lower productivity in the eastern GOA may be related to the limited shelf area in this part of the Gulf. Broader shelf areas such as that in the central Gulf of Alaska around Kodiak Island are generally believed to be more productive because of increased nutrient enrichment.

There is evidence from many areas around the world that high productivity is associated with a high biomass of demersal fishes and vice versa. For example, Farina et al. (1997) showed that on the continental shelf and upper slope in the Mediterranean Sea upwelling areas with high primary productivity correlate with a high biomass in the upper trophic levels, including demersal species, and with low species diversity. In contrast, low productivity areas have the greatest species richness and a smaller biomass of demersal fish. Our study suggests that the same general patterns observed by Farina et al. (1997) may hold for the continental shelf and upper slope of the GOA. The productive western GOA is characterized by a high demersal biomass and relatively low species diversity, which is attributable to the presence of a few highly abundant species of flatfish and gadids (including arrowtooth flounder, Pacific cod, walleye pollock). In contrast, the eastern GOA appears to be less productive and is characterized by a low biomass of demersal fishes and high species diversity, due to the presence of a large number of rockfish species with relatively low abundances.

[3] Kowalik, Z. 2000. Personal commun. Institute of Marine Sciences, University of Alaska Fairbanks, Fairbanks, Alaska 99775.

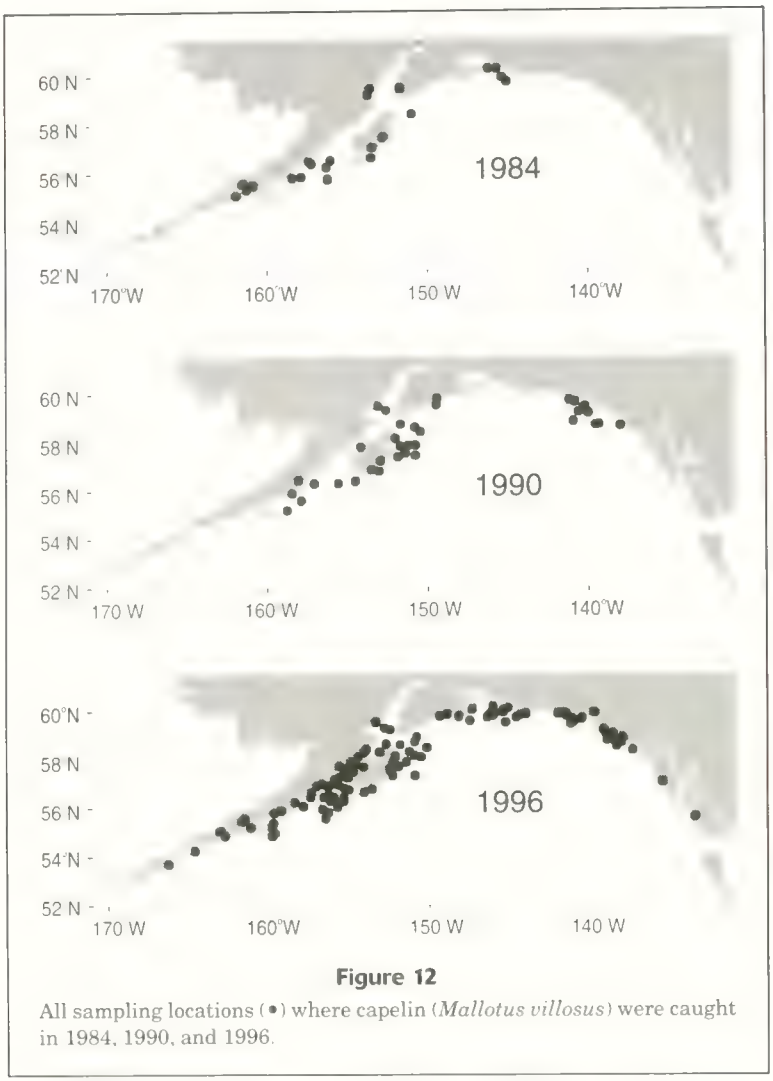

Figure 12

All sampling locations (•) where capelin (*Mallotus villosus*) were caught in 1984, 1990, and 1996.

In contrast to strong spatial and depth gradients, there was little evidence for strong temporal gradients in the GOA groundfish community between 1984 and 1996, except for the pronounced increase in total CPUE and a potential decrease in species diversity after 1993. The species composition of the groundfish community in the GOA, as reflected in our indices, has remained relatively stable from 1984 through 1996. Furthermore, a visual comparison of the indices mapped by year (not shown) suggests that relative species composition is characterized by spatial patterns that were stable from 1984 to 1996. Similarly, no apparent shifts in individual species distributions were found. The apparent stability of spatial patterns in the GOA may simply reflect stability in species composition over the time period of the study, as well as a period of relatively moderate variations in the physical environment. It also suggests that recent levels of fishing may not have had a strong impact on the relative species composition, or possibly had a stabilizing effect. The observed composition of the groundfish community, which is currently dominated by relatively long-lived species, may also contribute to its own stability.

Some of the most pronounced changes over time occurred in noncommercial species such as skates and capelin (Fig. 10). Whether these changes are directly or indirectly linked to fishing or are the result of environmental changes is currently unknown. Interestingly, capelin decreased in abundance in some areas and depth ranges but have been caught at an increasing proportion of the sampling stations in more recent surveys. These changes appear to reflect a "spreading out" of the population at relatively fixed numbers, possibly in response to the increasing abundance of large predatory fishes.

Other studies of groundfish communities have documented relatively stable spatial patterns in species composition over time periods of 10–20 years (Colvocoresses and Musick, 1984; Gabriel, 1992; Gomes et al., 1992; Jay, 1996). In contrast, Gomes et al. (1995) observed a sharp decline in the biomass and abundance of a number of commercial groundfish species on the Newfoundland-Labra-

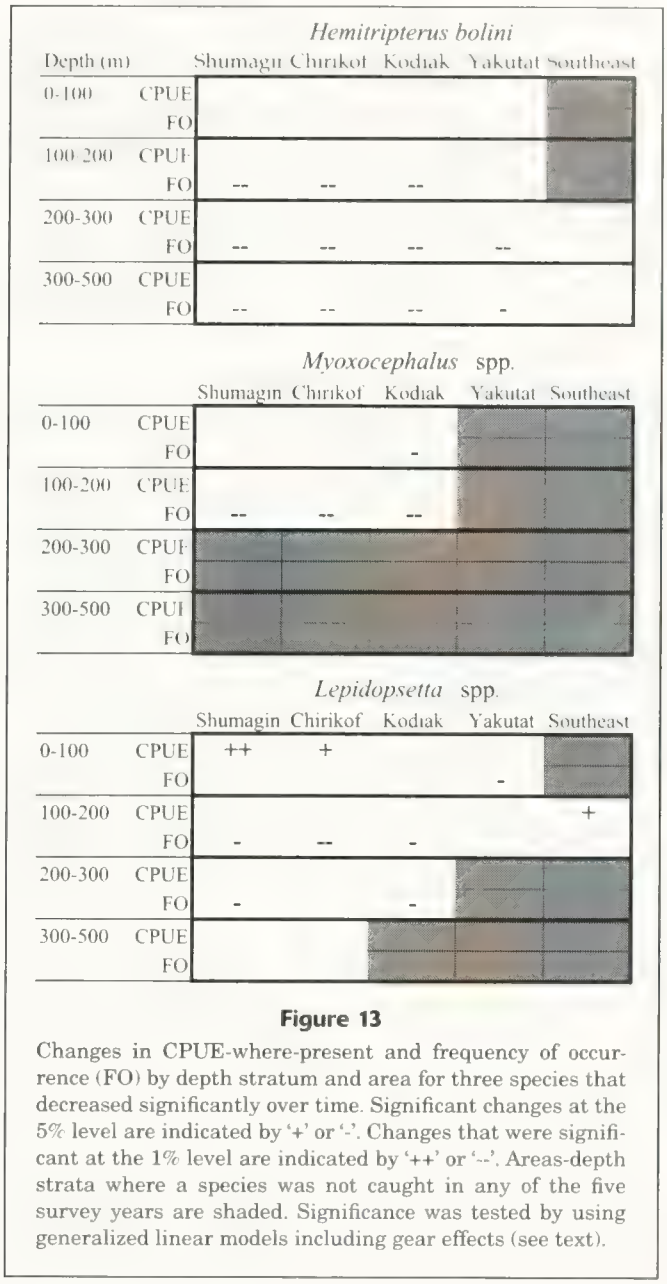

Figure 13

Changes in CPUE-where-present and frequency of occurrence (FO) by depth stratum and area for three species that decreased significantly over time. Significant changes at the 5% level are indicated by '+' or '-'. Changes that were significant at the 1% level are indicated by '++' or '--'. Areas-depth strata where a species was not caught in any of the five survey years are shaded. Significance was tested by using generalized linear models including gear effects (see text).

dor shelf from 1978 to 1991 and dramatic changes in the spatial distribution of groundfish assemblages after 1987. They attributed the changes primarily to intense exploitation, although environmental effects were likely at work as well. Similarly, on the continental shelf off Northwest Spain, significant decreases in commercial groundfish species, and a concurrent increase of several noncommercial species, can be attributed to a combination of fishing and environmental changes (Farina et al., 1997).

The recent period of stability in the GOA can be contrasted with a period of dramatic changes in the late 1970s and early 1980s that affected many parts of the North Pacific ecosystem including groundfish communities (e.g. Beamish, 1995). There is strong evidence of a shift in species composition of at least the nearshore demersal communities during this time period (Piatt and Anderson, 1996; Anderson and Piatt, 1999; Mueter and Norcross, 2000). Whether similarly dramatic changes occurred in offshore demersal communities is not known due to the lack of long time series for most species.

Estimated biomass trends for important commercial species based on recent stock assessment data (NPFMC[1]) and historical surveys (Ronholt et al.[4]) suggest that the

[4] Ronholt, L. L., H. H. Shippen, and E. S. Brown. 1978. Demersal fish and shellfish resources of the Gulf of Alaska from Cape Spencer to Unimak Pass 1948–1976: a historical review. Proc. rep., vols. 1–3, 872 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA.

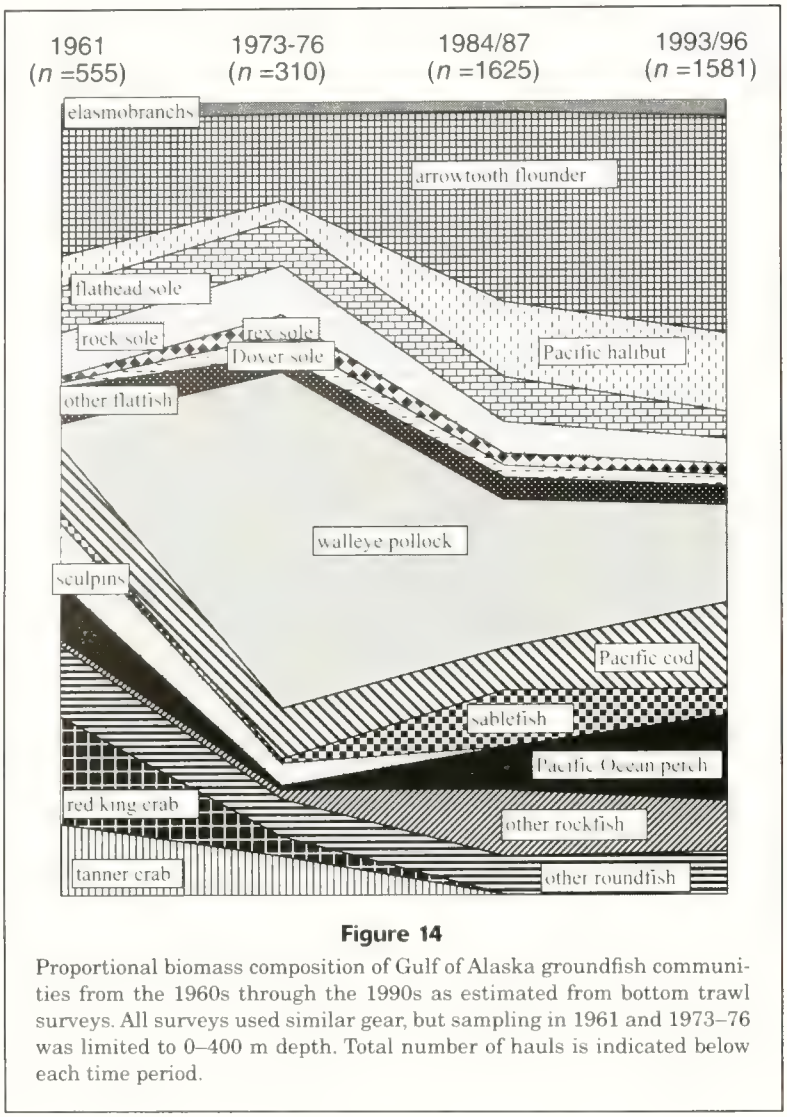

Figure 14

Proportional biomass composition of Gulf of Alaska groundfish communities from the 1960s through the 1990s as estimated from bottom trawl surveys. All surveys used similar gear, but sampling in 1961 and 1973–76 was limited to 0–400 m depth. Total number of hauls is indicated below each time period.

composition of the groundfish community on the shelf and upper slope has changed substantially since the early 1960s. Resource assessment surveys were conducted in 1961 and 1973–76 with similar gear and covering much of the same area that was sampled during the later surveys. Survey data from the 1960s and 1970s have to be interpreted carefully because the sampling design, gear, and the spatial coverage of these surveys differ from the surveys done in the 1980s and 1990s.[4] In particular, no stations below 400 m or east of 136°W were sampled in the early surveys. In spite of these caveats, changes in species composition among surveys are likely to reflect actual changes, at least for taxa that occur primarily above 400 m and west of 136°W. The data suggest a dramatic decrease in the relative abundance of red king crab (*Paralithodes camtschaticus*) and Tanner crab (*Chionoecetes* spp.), which together accounted for 22% of total CPUE in 1961, and for less than 1% after the 1970s (Fig. 14). The data indicated that walleye pollock became the dominant species in the mid-1970s, peaked in the early 1980s, and has declined in relative abundance since then. Arrowtooth flounder replaced walleye pollock as the dominant groundfish species in the 1980s and 1990s. Pacific Ocean perch and other rockfishes have increased substantially in biomass since the 1970s. Sablefish and Pacific halibut, two of the commercially most valuable species, made up a substantially larger proportion of the total CPUE in the 1980s and 90s compared to earlier decades (Fig. 14). The relative abundance of sculpins declined from about 8% in the early 1960s to less than 0.1% in the 1980s and 1990s. The observed difference is likely to reflect a real decline in sculpin abundance of several orders of magnitude between the 1960s and 1980s. The decline appears to continue into the 1990s, as suggested by a decrease in the frequency of occurrence and biomass of two of the most abundant sculpin taxa (bigmouth sculpin and *Myoxocephalus* spp., see Fig. 13, Table 2).

The observed increase in overall groundfish biomass in the GOA from the 1980s to the 1990s (Fig. 6) is consistent with increases in the productivity of the northeast Pacific

Ocean between the period of the 1960s and 70s and the 1980s and 90s. Polovina et al. (1995) suggested that the increase in primary and secondary productivity in the NE Pacific Ocean resulted from a shoaling of the mixed layer in the GOA by 20–30% associated with variations in the strength and position of the Aleutian low pressure system from the late 1970s to the late 1980s. Over the same time period large increases occurred in chlorophyll *a* levels (Venrick, 1995), zooplankton stocks (Brodeur and Pearcy, 1992; Brodeur et al., 1996), and upper trophic level species (Brodeur and Ware, 1995; Francis et al., 1998). Our study suggests that there has been a parallel increase in the biomass of demersal fish communities on the GOA shelf and upper slope since 1984, in response to the overall increase in productivity in the NE Pacific Ocean.

Given the increasing emphasis on ecosystem-based management, managers will have to rely on a variety of indicators in addition to traditional single-species biomass estimates to assess the status and health of an ecosystem (Yaffee et al., 1996). Indices of species composition like those used in this study, as well as survey-based assessments of noncommercial species, provide indicators that can help researchers in assessing changes in the community and can help managers in responding to such changes in a timely fashion.

Species richness and diversity are particularly simple, yet potentially very useful indices. The concept of marine biodiversity has received considerable attention in recent years (NRC, 1995) and should be included in planning and policy-making (Bengtsson et al., 1997). There is some evidence that bottom fishing can reduce the diversity of benthic communities (Collie et al., 1997) and, in turn, that changes in diversity can impact ecosystem function and productivity (Naeem et al., 1994). There was some indication in our study that the number of species and the diversity of the groundfish community in the GOA as measured by the Shannon-Wiener index decreased between 1993 and 1996 (Fig. 4). Although gear effects may have confounded differences among earlier surveys, the same gear and identical survey designs were used in both 1993 and 1996; thus the differences in species richness and diversity cannot be attributed to sampling effects and merit further study. The simple diversity indices used in our study were primarily chosen for practical considerations. Other indices, e.g. indices of beta-diversity, may be more appropriate for describing diversity of marine ecosystems and should be explored.

Multivariate techniques that summarize the major variation in species composition with a small number of indices (dimensions) provide another useful tool for monitoring changes in groundfish communities. Such indices provide sensitive indicators of change in community structure and can identify general trends that may not be apparent when using univariate measures (Austen and Warwick, 1989). The indices reduce the noise from random fluctuations of many individual stocks and the resulting "signal" may be used to test statistically for differences in species composition among areas or time periods, as well as helping to identify those species that show significant trends.

Another important part of an ecosystem approach to management is the monitoring of the abundance of noncommercial species, in addition to commercial species. Changes in the abundance of skates, sculpins, and other noncommercial species are examples of potentially important trends that may go undetected if management agencies focus on the assessment of commercial species only. Although these species comprise a small proportion of total biomass, such trends may be an early indication of changes in the groundfish community due to changes in the environment or fishing. Such monitoring, along with the monitoring of environmental variables, will further help to understand how and why groundfish communities change in response to environmental variation.

Current fisheries management often fails to account for the ecological complexities inherent in fish communities (Roberts, 1997). This is hardly surprising because of the focus of most stock assessment on individual stocks and on stock-recruitment relationships. Prediction becomes increasingly difficult as other species and environmental relationships are added to models. Nevertheless, the complexities should not discourage researchers from trying to understand species relationships and the response of species and communities to environmental variation and harvesting.

Knowledge of such relationships can improve management in several ways. First, it can help to explain why stocks are fluctuating in particular ways and help managers devise management strategies that take into account such fluctuations. Second, it can improve our understanding of multispecies or community-level relationships and can lead to better assessment methods that take such relationships into account. Third, it can lead to predictive hypotheses that can be explored and tested through rigorous research programs and adaptive management procedures. Ultimately, improved understanding of ecosystem processes will improve fisheries management only if it can reduce uncertainties in prediction. Thus the challenge remains to develop improved models that account for species relationships and environmental influences.

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Age, growth, mortality, and distribution of pinfish (*Lagodon rhomboides*) in Tampa Bay and adjacent Gulf of Mexico waters

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Abstract—Life-history dynamics of pinfish (*Lagodon rhomboides*) were examined from data derived from random-station surveys conducted in Tampa Bay and adjacent Gulf of Mexico waters during 1993–97. In addition, patterns in spatial distribution and abundance in Gulf of Mexico waters were investigated. Ages determined from whole otoliths ranged from 0 to 7 years, and von Bertalanffy growth models for males and females were not significantly different. Von Bertalanffy growth model parameters were L_∞=219.9 mm SL, k =0.33/yr, and t_0 =–1.10 years for all fish combined. High gonadosomatic indices during October–December indicated that some spawning may occur in Tampa Bay. Estimated lengths at 50% maturity were 132 mm SL for males and 131 mm SL for females. Total instantaneous mortality rates derived from the Chapman-Robson estimator ranged from 0.88 to 1.08/yr, and natural mortality was estimated to be 0.78/yr. In Gulf of Mexico waters, pinfish catch rates declined with increasing depth, and most pinfish were caught in <17 m of water. Length distributions showed that pinfish segregate by size with increasing depth.

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The pinfish (*Lagodon rhomboides*) is an ecologically important sparid that inhabits estuarine and offshore waters of the United States from Massachusetts to Texas (Darcy, 1985). Young-of-the-year pinfish are predators on a range of invertebrates in estuaries, often to the degree that entire assemblages of macrobenthic fauna are affected (Young et al., 1976; Young and Young, 1977; Nelson, 1978). They also consume seagrasses during their estuarine phase, which makes them an important link between primary and secondary production (Stoner, 1982; Weinstein et al., 1982; Montgomery and Targett, 1992). Both young-of-the-year and adult pinfish are prey for other fishes (Gunter, 1945; Darnell, 1958; Carr and Adams, 1973; Seaman and Collins, 1983) and are used as bait for many recreationally and commercially important species.

Despite their ecological and economical importance, the population biology and dynamics of pinfish in Florida have not been adequately examined. Most knowledge about growth (Reid, 1954; Caldwell, 1957; Hellier, 1962; Nelson, 1998), distribution and migration (Caldwell, 1957; Hansen, 1970; Nelson, 1998), and mortality (Nelson, 1998) comes from studies of young-of-the year pinfish in estuaries. The only information available on older individuals comes from estuarine studies that describe size and age at spawning (Caldwell, 1957; Hansen, 1970), gross fecundity (Caldwell, 1957), and longevity and size at age (Hansen, 1970). However, that information may contain biases because sampling did not extend into offshore waters where larger, and presumably older, pinfish are thought to occur, particularly during cooler months (Darcy, 1985).

In this study, age, growth, mortality, and maturation of pinfish were evaluated by studying data from multigear fisheries-independent surveys conducted in Tampa Bay, Florida, and in offshore waters off west-central Florida. In addition, patterns in abundance and spatial distribution of pinfish in the Gulf of Mexico were examined.

Methods

Biology

Pinfish for aging, maturity, and mortality analyses (n=711) were collected opportunistically from fall 1993 to spring 1997 during multiple fisheries surveys conducted in Tampa Bay and offshore Gulf waters by the Florida Marine Research Institute (Fig. 1). Pinfish from Tampa Bay were collected primarily during multigear seasonal (spring and fall) and monthly fisheries-independent surveys designed to estimate relative abundance of small estuarine fishes and evaluate life-histories parameters of large estuarine fishes (Table 1). During the surveys, sites were chosen by randomly selecting 1″ latitude × 1″ longitude microgrids, representing the site to be sampled, within randomly selected 1′ latitude ×

Table 1

Length summary statistics (by area, year, and gear) for pinfish collected during biological sampling. Exp. gill net = experimental gill net.

Year	Gear	Stretched mesh (mm)	Pinfish SL (mm)			
			Minimum	Maximum	Mean	*n*
Tampa Bay						
1993	trammel net	76, 305	179	255	211.8	31
1995	exp. gill net	50–152	170	185	180.0	3
	183-m seine	38	73	202	121.1	50
	trammel net	76, 305	173	216	191.4	8
	21-m seine	3.2	73	150	112.1	24
	61-m seine	25.4	72	165	132.6	19
1996	183-m seine	38	66	207	126.9	313
	purse seine	50	100	181	125.9	34
	trammel net	76, 305	203	203	203.0	1
	21-m seine	3.2	34	174	89.0	28
	hook and line	—	198	205	202.0	3
1997	183-m seine	38	83	155	111.3	62
	purse seine	50	91	156	108.9	16
	21-m seine	3.2	25	104	71.7	18
Gulf of Mexico						
1996	hook and line	—	116	149	135.2	17
1997	bottom trawl	254	95	175	128.8	84

1′ longitude grids. At each site, gears were deployed with standardized procedures (see Nelson [1998] and Tremain and Adams [1995] for detailed description of the survey design and deployment techniques). Selected individuals were immediately placed on ice for transport and frozen whole at the laboratory.

Pinfish from the Gulf of Mexico were collected primarily during a bottom-trawl survey conducted in spring in the Gulf of Mexico to document baitfish abundance and distribution. The Gulf trawl survey was conducted during April from 1994 to 1997 at stations randomly selected along line transects randomly placed perpendicular to the west coast of the Florida peninsula adjacent to Tampa Bay. At each station, a 19.8-m, 254-mm stretched-mesh modified ballon trawl with 25.4-mm codend liner and 2.2-m^2 China V-doors was towed at approximately 3 knots for 30 min during daylight hours in depths ranging between 6 and 31 m. At each station, trawl catches were sorted by species, counted, weighed collectively, and 50 individuals per haul were measured to the nearest 1 mm fork length (see Pierce and Mahmoudi [2001]) for a detailed description of the survey design). Depth (m) at the start and end of the trawl tow and surface salinity and temperature were recorded at all stations. To match data collected from the Tampa Bay samples, all length data were converted to standard length by using conversion equations derived from this study. Individual fish were immediately frozen whole and returned to the laboratory. Occasionally, supplemental samples were collected by hook-and-line fishing in Tampa Bay and the offshore waters (Table 1).

Figure 1

Maps of Florida showing study area.

In the laboratory, standard length (SL ±1 mm), fork length (FL ±1 mm), total length (TL ±1 mm) and total

weight (TW ±0.01 g; measured after each individual was blotted dry) were recorded for all thawed, undamaged individuals. Gonads were excised from a subsample of individuals (~80%) of each collection, identified macroscopically (and microscopically if needed) as ovaries or testes, blotted dry on a paper towel, and weighed (±0.01 g). Seasonal conversion equations for length measurements were generated by least-squares regression (SAS, 1990a).

Age and growth

Sagittal otoliths for aging studies were excised, cleaned of extraneous tissue, and stored dry in vials. Otolith length was measured under a binocular dissecting microscope at 10× with a calibrated ocular micrometer, and an otolith length (mm) versus fish standard-length relationship was derived by using least squares regression. For age determination, one whole otolith (either left or right) was placed on black velvet to enhance the visibility of opaque zones, submerged in a 60% glycerin solution, and viewed at 32× with reflected light. Otolith edges were classified as either opaque or hyaline to determine time of opaque ring formation. The number of opaque rings was considered to equal the age in years of the pinfish. Age determinations were repeated three times on all whole otoliths. If two of the three age readings were in agreement, the value was accepted. If age varied between all readings, the structure was not included in the analysis. The accuracy with which whole otoliths can be used to age pinfish was confirmed by comparing whole otolith ages from a subsample of the largest pinfish to age readings made on thin sections of the same otoliths. Methods of Hood and Johnson (1999) were used to section otoliths. To verify the consistency of the opaque ring counts, a random subsample (13%) of all whole otoliths was aged once by an experienced second reader and the results were compared to the final age determination. Pinfish larvae are present off the west coast of Florida between November and February (Darcy, 1985); therefore a 1 January birthdate was assumed for all pinfish. Age in years was designated with a decimal extension that represented the date of capture in days from the 1 January birthdate.

Growth was modeled by fitting length-at-age for all years combined to the von Bertalanffy equation:

$$L_{i,t} = L_\infty \left(1 - \exp^{-k(t - t_0)}\right) + \varepsilon_i,$$

where $L_{i,t}$ = the standard length of the i th individual at age t;
L_∞ = the asymptotic maximum length;
k = a growth constant;
t_0 = the hypothetical age at which length is zero; and
$\varepsilon_i s$ = independent, identically distributed, normal random errors.

Parameters L, k, and t_0 were estimated by using SAS nonlinear regression (Proc NLIN) with the Marquardt method (SAS Institute, 1990b). Lack of fit was assessed by using residuals plots (Bates and Watts, 1988).

Growth-rate differences between sexes were investigated by using an approximate randomization test to compare growth curves (Helser, 1996). Essentially, differences were investigated by comparing an observed test statistic to an empirical probability density function of a test statistic under the null hypothesis of no difference. The observed test statistic for pinfish was developed by fitting the von Bertalanffy growth functions to length-at-age data for sexes combined and to length-at-age for each sex separately. The sums of the residual sum of squares from the two sex-specific models were then used to calculate the observed test statistic

$$t(x_0) = \sum_{i,t} (l_{i,t} - \hat{l}_t)^2 - \sum_{i,t,p} (l_{i,t,p} - \hat{l}_{t,p})^2,$$

where $t(x_0)$ = the test statistic;
l_t = the predicted length-at-age for all sexes combined; and
$l_{t,p}$ = the predicted length-at-age for each sex (p=1,2) (Helser, 1996).

To generate the empirical probability density function (pdf), length-at-age data for both sexes were pooled and then assigned randomly without replacement to two groups with sample sizes equal to the original number of observations per sex. Growth curves were then fitted separately to the length-at-age data of the randomized groups, and the test statistic under the null hypothesis of no difference was calculated as

$$t(x) = \sum_{i,t} (l_{i,t} - \hat{l}_t)^2 - \sum_{i,t,p} (l_{i,t,p} - \hat{l}_{t,p})^2,$$

where $t(x)$ = the difference in residual sum of squares between the von Bertalanffy fits to the entire pooled data set and von Bertalanffy fits to the randomized groups (denoted by *).

The randomization procedure was repeated 1000 times to obtain the pdf of $t(x)$. The null hypothesis of no difference was rejected if $t(x_0) > t(x)$ at α=0.05.

Reproduction, sex ratios, and maturity

Gonads excised from selected individuals were classified macroscopically as either immature or mature by using the maturation criteria of Nikolsky (1963) and Cody and Bortone (1992). Seasonality of reproduction was determined by noting when changes in the gonad condition took place. A gonadosomatic index (GSI) was calculated to show changes in gonad weight in relation to gonad-free total body weight. The index was computed as

$$GSI = gonad\ weight / (total\ body\ weight - gonad\ weight) \times 100.$$

Length at 50% maturity was estimated for pinfish captured during the season of gonadal maturation. The prob-

ability of pinfish being mature was modeled as a logistic function of the following form:

$$P_i = \frac{\exp^{(\alpha+\beta x_i)}}{1+\exp^{(\alpha+\beta x_i)}} + \varepsilon_i,$$

where P = the response probability;
x = the standard length (mm) of the i th fish;
α = the intercept;
β = the slope coefficient of standard length; and
ε_i = the error term.

Model regression coefficients were estimated using maximum likelihood (SAS, 1997). Goodness-of-fit was assessed with the chi-square test.

Chi-square analyses were used to test for deviations from a theoretical 50:50 sex ratio.

Length-weight relationships

Because of the seasonality of reproduction, data on body length and weight were separated into two groups representing two time periods to construct length-weight relationships that reflected seasonal changes in gonad weight. Data collected during March–August composed the data group representing the spring–summer period, and data collected during September–February composed the data group representing the fall–winter period. Seasonal regression equations for $\log_{10}$-transformed standard length and body weight (total and gonad-free weight) were generated by the least-squares regression. One-way analysis of covariance (Sokal and Rohlf, 1981), conducted by using SAS PROC MIXED (Littell et al., 1996), was used to test for differences between regression slopes and adjusted means of the length-weight relationships by sex and season.

Mortality

Total instantaneous mortality (Z) was estimated in Tampa Bay and the Gulf of Mexico from pinfish numbers-at-age data by using the Chapman-Robson equation for survival (S) estimation:

$$-Z = \ln(S) = \ln\left(\frac{\sum_{i=1}^{n} x_i}{n + \sum_{i=1}^{n} x_i - 1}\right),$$

where ln = the natural log;
x_I = the number of years the i th fish is older than the age-at full-recruitment;
S = annual survival; and
n = the total number of fully recruited fish (Chapman and Robson, 1960).

The variance of Z was estimated from the variance of S by

$$V(Z) = \frac{S(1-S)}{n-S^2}$$

(Jensen, 1985). The Chapman-Robson estimator was used because it is more robust to sample size variation in numbers-at-age (Jensen, 1996; Murphy, 1997).

In addition to Z, natural mortality (M) of pinfish was estimated by using a multiple regression equation relating M to L_∞ (TL in cm) and k (per yr) of the von Bertalanffy equation, and to mean annual water temperature (°C)(Pauly, 1980). To estimate the growth parameters used in the equation, the von Bertalanffy function was refitted to total length and age data. Mean annual water temperature was estimated from temperature data of the Tampa Bay survey.

Distribution

To determine if pinfish catch rates in the Gulf of Mexico were associated with depth, a generalized linear model (McCullagh and Nelder, 1989) was used to model the random trawl catches during the April survey from 1994 to 1997. Catch data were transformed by using $\ln(x+1)$ to stabilize the variance and reduce the influence of sampling variability between tows. Year, average depth of the trawl tow, and their first-order interaction were included in the model. Only depth was analyzed because surface readings of temperature and salinity were thought to not reflect bottom conditions where the trawl tows were made. Size structure of pinfish caught during the Gulf of Mexico survey was also examined by calculating summary statistics (mean and percentiles) of length data to identify patterns related to depth.

Results

Biology

Length-conversion equations are listed in Table 2. All slopes and intercepts were significantly different from zero.

Age and growth

Age determination was based on sagittae from 658 pinfish (66–255 mm SL). Alternating opaque and hyaline zones, which composed an annual growth increment, were evident on whole pinfish otoliths (Fig. 2A). Only 13 otoliths were considered unreadable. Agreement between the number of opaque bands counted on whole otoliths and the number counted on sections of the same otoliths (Fig. 2B) was 96.3% (26/27), indicating that whole otoliths can be used to reliably age pinfish. The high percentage of agreement (89.6%) between the author's final annulus counts and those made by a second reader, and no apparent bias towards a particular aging error, indicated that ages were consistently interpreted.

Plots of the monthly proportions of otolith with opaque edges for pinfish ages 1 to 3 indicated that an opaque ring

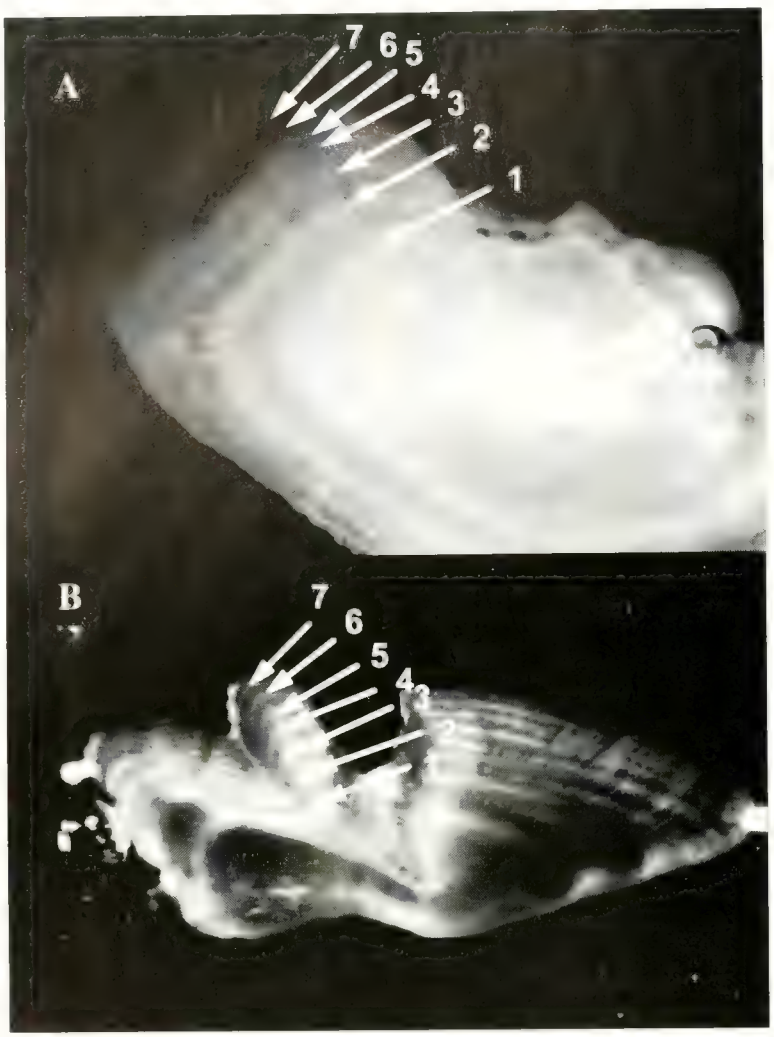

Figure 2

A whole (**A**) and sectioned (**B**) sagitta from a 7-year-old (230-mm-SL) pinfish caught in Tampa Bay in November 1993.

is formed only once a year, during late winter to late spring. Deposition of opaque material began as early as January; it peaked during March, April, or May depending on age; and it was completed, or nearly so, by June (Fig. 3).

A single regression equation characterized the relationship between otolith length (OT in mm) and standard length for a random sample of pinfish 71–230 mm SL (standard errors are in parentheses) used in age analysis:

$$OT = 8.03(1.07) + 0.39(0.008) \times SL; \quad [r^2 = 0.95, n = 132].$$

The intercept and slope coefficients were significantly different from zero ($P<0.001$).

Ages of pinfish ranged from 0 to 7 years (66–255 mm SL) in Tampa Bay and from 1 to 6 years (95–175 mm SL) in the Gulf of Mexico (Fig. 4A). The majority (88.1%) of aged pinfish were ≤2 years. Residual plots from the growth models showed near-random patterns, indicating that the von Bertalanffy model adequately described the growth of male and female pinfish. Results of the randomization test did not indicate a significant difference between male and female growth models ($t(x_0)$=2,691; $p(t(x)>t(x_0))$=0.27); therefore, a von Bertalanffy model was fitted to all pinfish data combined (Fig. 4B, Table 3). Growth rate of pinfish was rapid for the first 1–3 years of life but gradually decreased thereafter (Fig. 4B).

Reproduction, maturity, and sex ratios

Seasonality of reproduction was indicated by monthly changes in the GSIs of all pinfish over time. In Tampa Bay and the Gulf of Mexico, GSIs for males and females were ≤0.5% during the spring and summer months (Fig. 5).

Table 2

Linear regression statistics showing the length conversion and length-weight relationships for pinfish. For the length conversions, the model is $y = \alpha + \beta \times x$. For the weight-length relationships, the model is $\log_{10}(y) = \alpha + \beta \times \log_{10}x$. α is the regression intercept, β is the slope coefficient, r^2 is the coefficient of determination, n is the sample size, MSE is the mean square error, FL is fork length (mm), SL is standard length (mm), TL is total length (mm), GFW is gonad-free body weight, and TW is total body weight (g). SP–SU is spring–summer and FA–WI is fall–winter. All slopes and intercepts were significantly different ($P \leq 0.05$) from zero. Slopes between TW-SL relationships were significantly different ($P \leq 0.01$).

y	x	Season	α	SE(α)	β	SE(β)	r^2	n	MSE
FL	SL	All	2.65	0.368	1.14	0.003	0.996	603	4.736
TL	SL	All	–2.20	0.542	1.33	0.004	0.994	625	13.745
TL	FL	All	–3.73	0.412	1.15	0.003	0.997	591	5.695
GFW	SL	SP–SU	–4.56	0.061	3.04	0.029	0.977	257	0.0020
TW	SL	SP–SU	–4.53	0.045	3.03	0.021	0.983	343	0.0020
GFW	SL	FA–WI	–4.57	0.064	3.07	0.030	0.977	244	0.0024
TW	SL	FA–WI	–4.68	0.043	3.11	0.021	0.987	302	0.0023

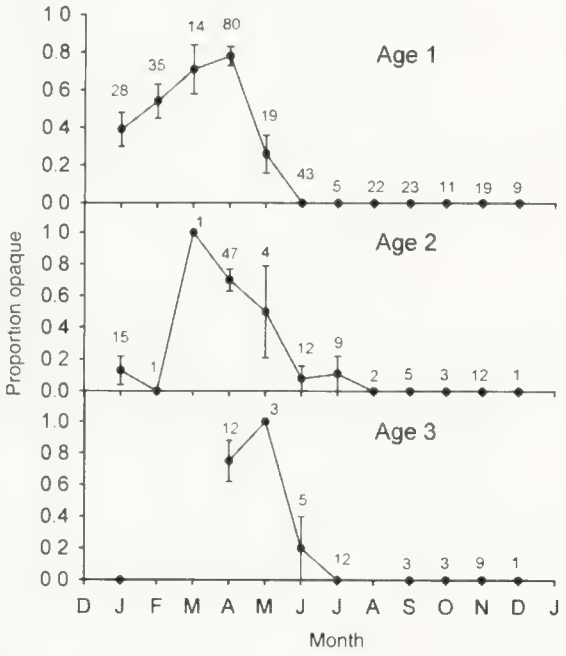

Figure 3

Monthly proportions of whole otoliths with opaque edges for pinfish ages 1–3. ±1 standard error bars are shown.

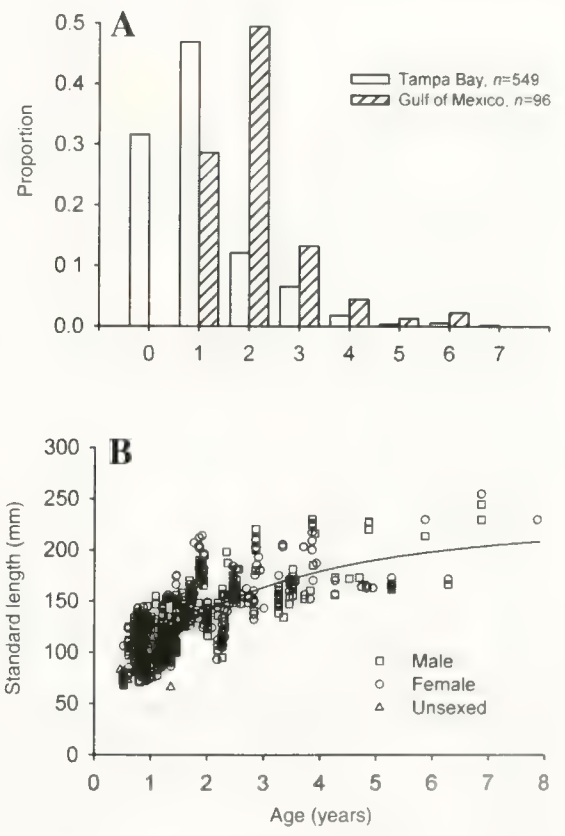

Figure 4

Plots of (**A**) age composition from Tampa Bay and Gulf of Mexico samples and (**B**) von Bertalanffy growth model fitted to standard length and age data for all sexes combined.

GSIs began to increase in October (females) and November (males) in Tampa Bay. The highest GSIs for males and females in Tampa Bay were 5% and 8%, respectively, observed in December. High and moderate GSIs for females and males during January in the Gulf of Mexico indicated continued spawning, but low values in April suggested that spawning ended prior to that month (Fig. 5).

Maturity of male and female pinfish was related significantly to length (male: Wald χ^2=18.8, $P \leq 0.001$; female: Wald χ^2=32.1, $P \leq 0.001$) by logistic equations, and there was no evidence of lack of model fit (male: χ^2=81.1, df=94, P=0.82, max-rescaled r^2=0.38; female: χ^2=109.2, df=121,

Table 3

Estimates of the von Bertalanffy growth parameters for pinfish by sex and for all sexed and unsexed fish combined. MSE is the mean square error, r^2 is the coefficient of determination, and n is the sample size. Asymptotic standard errors are shown in parentheses.

Sex	L_∞	k	t_0	MSE	r^2	n
Male	228.5 (19.733)	0.31 (0.079)	–1.21 (0.331)	517.926	0.57	285
Female	212.0 (16.504)	0.33 (0.082)	–1.16 (0.309)	551.020	0.51	330
All fish	219.9 (12.204)	0.33 (0.055)	–1.10 (0.203)	537.490	0.55	645

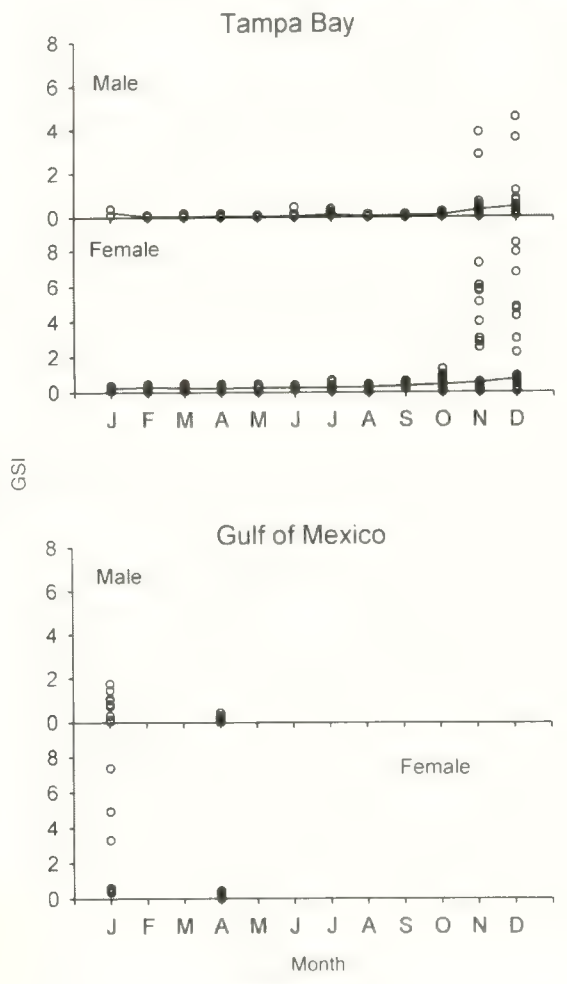

Figure 5

Plots of monthly gonadosomatic indices (GSI) for male and female pinfish from Tampa Bay and the Gulf of Mexico. The solid line connects median values.

P=0.77, max-rescaled r^2=0.60). Parameter estimates (standard error) were α = –7.78 (1.745) and β = 0.06 (0.014) for males, and α = –9.83 (1.721) and β = 0.08 (0.013) for females. The estimates of length at 50% maturity ±95% C.I. were similar for both sexes: 132 ±8 mm SL for males and 131 ±8 mm SL for females. The smallest mature male was 112 mm SL and the smallest mature female was 92 mm SL. The largest immature male pinfish was 245 mm SL and female pinfish was 173 mm SL.

Chi-square tests indicated that sex ratios did not deviate significantly (P>0.05) from unity in any season.

Length-weight relationships

No significant differences (P≥0.10) in slopes or intercepts of standard-length on body-weight relationships were observed between sexes in any period; therefore all data were pooled for the subsequent analyses. Seasonal length-weight regressions for both sexes combined are listed in Table 2 for total and gonad-free body weight. Regression slopes were significantly different between periods only for the standard-length on total-body-weight relationship (P≤0.01). The regression slope was highest in fall–winter, which indicates that pinfish gain more weight per unit increase in length during this period than in spring–summer. Adjusted means for the standard-length on gonad-free body-weight relationship were not significantly different between periods (P>0.05).

Mortality

Based on frequency plots by age, age-at-full-recruitment was age 1 for pinfish in Tampa Bay and age 2 for those in the Gulf of Mexico. Estimates of Z were 1.08/yr for Tampa Bay pinfish and 0.88/yr for the Gulf of Mexico pinfish (Table 4). Estimates of Z for all areas combined, assuming full recruitment at age 2, were intermediate to the Z estimates made for each area separately (Table 4).

The estimate of M was 0.78/yr from Pauly's (1980) multiple regression equation by using L_∞ = 30.1 cm, k=0.31/yr, and mean annual temperature of 24°C.

Distribution

In the Gulf of Mexico, pinfish were captured at 90% (55/61) of sites where trawls were pulled in depths of 6 to 30 m during the baitfish survey (Fig. 6). Catch rates of pinfish in the Gulf of Mexico varied significantly between years and were associated with depth, but the significant interaction term indicated that the relationship between depth and catches varied between years (Table 5). Plots of cumulative proportions of total catches by year showed that most trawl catches (95%) occurred in waters <15 m during the 1994, 1995, and 1997 surveys, but in 1996, 95% occurred in waters <17 m (Fig. 7A).

Length summary plots for pinfish caught during the baitfish survey showed that pinfish became segregated by size as depth increased. Median length increased from 109 mm SL in the 6–10-m depth range to 152 mm SL in the 26–30 m depth range (Fig. 7B). The smallest (80-mm-SL)

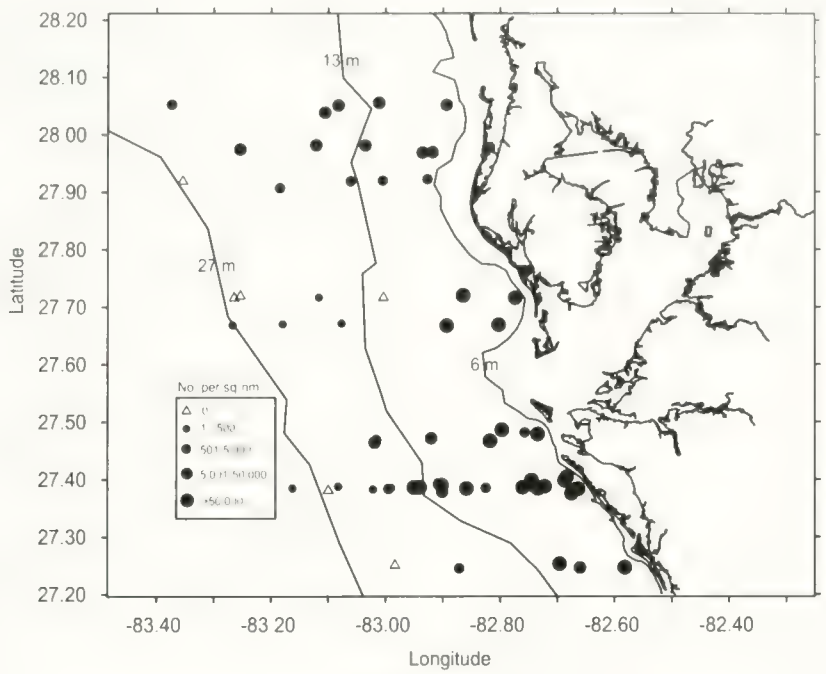

Figure 6

Map of distribution of pinfish catches from the baitfish trawl survey in Gulf of Mexico waters adjacent to Tampa Bay, 1994–97. Latitude and longitude values are given in decimal degrees.

Table 4

Estimates of annual survival (S) and total instantaneous mortality (Z) of pinfish determined by using the Chapman-Robson (1960) estimator for Tampa Bay, the Gulf of Mexico, and both areas combined. n_r is the sample size at each age of full recruitment and n_a is the number of age classes included.

	Age (yr) at full recruitment	n_r	n_a	Estimate		Variance	
				S	Z	S	Z
Tampa Bay (n=549)	1	379	7	0.34	1.08	0.0004	0.0033
Gulf of Mexico (n=96)	2	70	5	0.41	0.88	0.0020	0.0120
Combined (n=645)	2	189	6	0.40	0.90	0.0008	0.0043

and the largest (203-mm-SL) pinfishes were captured in the 6–10 m and 11–15 m depth ranges, respectively.

Discussion

Age and growth

This study is the first to report otolith-derived age estimates for pinfish. Hansen (1970) reported scale-derived age estimates for pinfish from a Florida Panhandle estuary. In the current study, annuli were identified and counted on whole otoliths and were then identified and counted on thin sections. The high initial agreement (89.6%) between the age determinations of the author and a second reader suggests a high degree of precision can be attained without sectioning the otolith. Given the high degree of error generally associated with estimating ages of fish from their scales (Jearld, 1983; Beamish and McFarlane, 1987), I believe that age estimations made from pinfish otoliths are far more likely to be accurate.

Deposition of opaque material in the sagittal otoliths of pinfish occurs over a protracted late-winter to early-spring period and indirectly validates the formation of annuli in

Table 5

Results of the generalized linear model analysis of ln (x+1) pinfish catches (in number per nmi^2) from the baitfish cruises in the Gulf of Mexico, 1994–97. ***=$P \leq 0.001$.

Source	df	MS	F	r^2
Model	7	79.9	16.1***	0.680
Year	3	25.5	5.1***	
Depth	1	389.3	78.4***	
Year × depth	3	31.3	6.3***	
Error	53	5.0		
Corrected total	60	13.7		

pinfish. Similarly, Hansen (1970) found that annuli on scales are generally formed once a year, in April.

The maximum age of pinfish determined in this study was 7 years, which exceeded the maximum age of 2 years reported by Hansen (1970). The difference in maximum age is probably due to Hansen's inadequate sampling of the entire size range of pinfish in Pensacola Bay—he collected pinfish at only two stations using a single, selective trawl. In addition, Hansen's use of scales as the primary aging structure may have contributed to the underestimate of the maximum age of pinfish (Beamish and McFarlane, 1987). In contrast, pinfish collected in this study were sampled from numerous locations in Tampa Bay and adjacent Gulf waters with multiple types of gears that had various mesh sizes, and otoliths, which are more reliable aging structures than scales (Beamish and McFarlane, 1987), were used for age determination. Coincidentally, Caldwell (1957) projected from the growth rates of age-1 pinfish that a 328-mm-SL pinfish may have been as old as 7 years; my results provide direct evidence that supports his estimate.

Reproduction, sex ratios, and maturity

The monthly changes in GSIs show that pinfish are late-autumn to early-spring spawners in Tampa Bay and adjacent Gulf of Mexico waters; this conclusion was also reported by Darcy (1985) and Cody and Bortone (1992). Pinfish spawning is suspected to occur in offshore oceanic waters (Hansen, 1970; Darcy, 1985); however, the high GSIs of pinfish collected in Tampa Bay and the occurrences of several of these pinfish with late-developing gonads in waters about 3–6 km into the bay during October–December suggest that some spawning activity may occur in this estuary. This is not surprising because most studies that have examined gonadal activity in pinfish have used samples only from offshore waters (Franks et al., 1972; Stott et al., 1980, 1981), did not use gear with various mesh sizes to adequately sample the entire size range of pinfish found in estuaries (Caldwell, 1957; Hansen, 1970), or did not compare data on an estuary-offshore basis (Cody and Bortone, 1992).

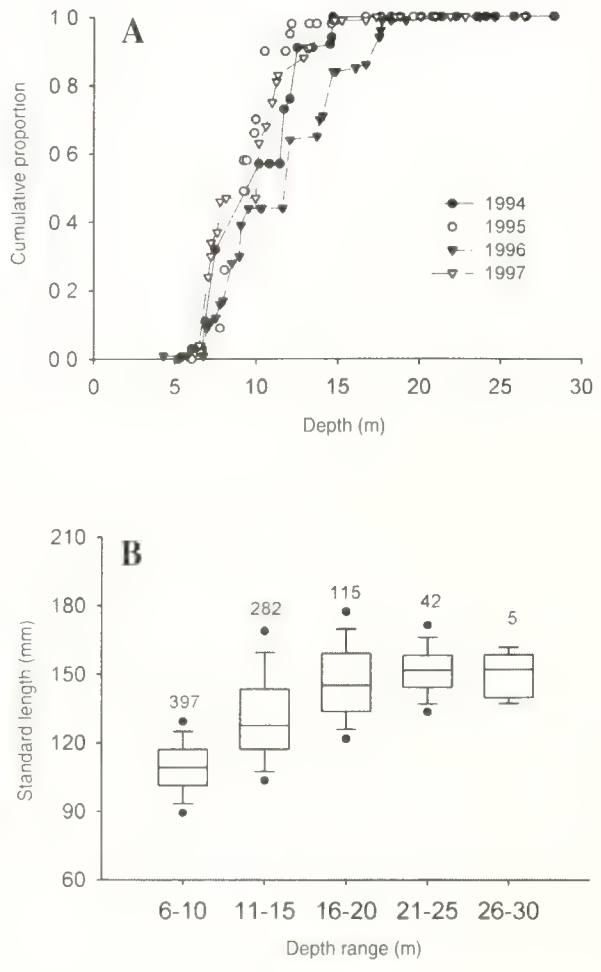

Figure 7

Plots of (**A**) cumulative catch versus depth by year and (**B**) size frequency of pinfish by depth range from the baitfish trawl survey, 1994–97. In B, the lower and upper dots represent the 5th and 95th percentiles of the length distribution, the whiskers represent the 10th and 90th percentiles, the box represents the 25th and 75th percentiles, and the horizontal line represents the median length.

Length-weight relationships

The length-weight relationships were affected by gonadal maturation. During the September–February period, gonad weight of both sexes increased, which resulted in a standard-length to total-body-weight relationship that was higher than it was in March–August period. Differences in predicted total weight at length were 2–8% between the September–February and March–August periods and illustrate the effect of maturation on these relationships. The slopes of the length-weight relationships from both periods (3.03–3.11) were higher than the slopes of length on weight relationships (2.91 and 2.90, respectively) developed by Caldwell (1957) and Cameron (1969).

Mortality

This study is the first to report total instantaneous mortality (Z) rates (0.88–1.08) for pinfish older than young-of-the-year. It is difficult to conclude whether the mortality rate in Tampa Bay is really higher than that in the Gulf. The small mesh characteristics of the sampling gear, the restricted spatial coverage of sampling from Tampa Bay to the shallows of the estuary where young pinfish dominate (most gears were employed in waters <3 m), or the migration of pinfish from estuaries to offshore waters to spawn may have contributed to the older (>age 1) fish being underrepresented in the sampling of bay waters (Hansen, 1970; Darcy, 1985; Nelson, 1998). By assuming that pinfish are fully recruited at age 2 (Table 4), I estimated that Z from data for both areas combined is probably more realistic because the numerical proportions of pinfish ages 2 and older in Tampa Bay were nearly identical to the numerical proportions of pinfish age 2 and older from the Gulf of Mexico. The estimate of Z from data for both areas combined (0.90/yr) was close to the natural mortality estimate of 0.78/yr, suggesting that the portion of annual mortality attributed to fisher activity, calculated by $(Z–M)/Z$, is low [13%].

Distribution

Darovec (1995), Franks et al. (1972), and Darcy and Gutherz (1984) reported that pinfish from the Gulf of Mexico occurred in trawls to depths between 73 m and 93 m. However, most pinfish captured in Gulf waters off west-central Florida were captured from depths <19 m (Darovec, 1995). The results from the baitfish survey were very similar in that most pinfish (95%) were caught in waters <17 m, but the abundance-depth relationship varied between years, and larger pinfish were generally associated with greater depths. The propensity of pinfish to limit their depth distribution and alter their size distribution with depth is probably due to the distribution of their epibenthic prey (Stoner, 1980; Nelson and Bortone, 1996), the distribution of their predators, and (because pinfish are visual feeders) reduced light intensity with depth (Kjelson and Johnson, 1976; Luczkovich, 1988).

In summary, ages determined from whole otoliths ranged from 0 to 7 years, and von Bertalanffy growth model parameters for all aged fish were L_{∞}=219.9 mm SL, k =0.33/yr, and t_0 =–1.10 years. High gonadosomatic indices during October–December indicated that some spawning may occur in Tampa Bay. Estimated lengths at 50% maturity were 132 mm SL for males and 131 mm SL for females. Total instantaneous mortality rates from the Chapman-Robson estimator ranged from 0.88 to 1.08/yr, and natural mortality based on Pauly's (1980) equation was 0.78/yr. Catch rates of pinfish were related to depth in the Gulf of Mexico.

Acknowledgments

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Recovery of the Gulf of Maine–Georges Bank Atlantic herring (*Clupea harengus*) complex: perspectives based on bottom trawl survey data

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Abstract—NMFS bottom trawl survey data were used to describe changes in distribution, abundance, and rates of population change occurring in the Gulf of Maine–Georges Bank herring (*Clupea harengus*) complex during 1963–98. Herring in the region have fully recovered following severe overfishing during the 1960s and 1970s. Three distinct, but seasonally intermingling components from the Gulf of Maine, Nantucket Shoals (Great South Channel area), and Georges Bank appear to compose the herring resource in the region. Distribution ranges contracted as herring biomass declined in the late 1970s and then the range expanded in the 1990s as herring increased. Analysis of research survey data suggest that herring are currently at high levels of abundance and biomass. All three components of the stock complex, including the Georges Bank component, have recovered to pre-1960s abundance. Survey data support the theory that herring recolonized the Georges Bank region in stages from adjacent components during the late 1980s, most likely from herring spawning in the Gulf of Maine.

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Fish. Bull. 100:593–608 (2002).

The Atlantic herring (*Clupea harengus*) resource in the Northwest Atlantic has been an important source of food and commerce for nearly four centuries (Anthony and Waring, 1980). Simple wier fisheries with relatively low landings began in the 1600s in both the United States and Canada but evolved into much larger operations, and landings increased. The most important early fishery for herring in the United States developed in the late 1800s, resulting in the building of numerous sardine canning plants, with annual landings eventually ranging from 60,000 metric tons (t) to 100,000 t by the early to mid 1900s (Anthony and Waring, 1980). An important weir fishery developed in New Brunswick during the 1950s and provided fish for canning operations in the region. Both the U.S. and Canadian fisheries initially focused on juvenile fish; fisheries for adults developed only when the abundance of juveniles (available to fixed gear) declined in the early 1960s (Anthony and Waring, 1980).

In the early 1960s Atlantic herring on Georges Bank became the focus of a major fishery by gill-net vessels from the former Soviet Union (Hennemuth and Rockwell, 1987). By the mid 1960s distant-water herring fisheries had developed in the Gulf of St Lawrence, on the Scotian Shelf, on Georges Bank, and on Jeffreys Ledge (Fig. 1) (Anthony and Waring, 1980). Landings of herring from the Gulf of St Lawrence to Georges Bank peaked at over 900,000 t in 1968, declining steadily thereafter (Anthony and Waring, 1980).

The Georges Bank herring fishery (combined Nantucket Shoals and Georges Bank region) began in 1961 and increased rapidly to a peak of 373,000 t in 1968 (Figs. 1 and 2). During the early 1970s, landings steadily declined and in 1977 the herring fishery on Georges Bank collapsed (low landings and abundance) (Fig. 2) (Anthony and Waring, 1980; Tupper et al.[1]). During the same period, landings in the Gulf of Maine fishery ranged from 35,000 to 82,000 t (Fig. 2).

Stock assessments prepared by the International Commission for Northwest Atlantic Fisheries (ICNAF) for Georges Bank herring (combined Nantucket Shoals and Georges Bank) began in the late 1960s, and annual total allowable catch quotas (TAC) were established in 1972. Annual assessments were conducted by using virtual population analysis (VPA) and results from these assessments revealed that the Georges Bank component peaked in abundance in 1967 and rapidly declined thereafter (Anthony and Waring, 1980). These findings were confirmed by larval herring surveys conducted during the 1970s and 1980s, where a general decline in larval abundance in the region was noted during 1975–78 and the complete absence of herring larvae in the Georges Bank-Nantucket

[1] Tupper, M. H., V. C. Anthony, S. B. Chenoweth, and H. A. MacCluen. 1998. Biology and assessment of Gulf of Maine herring stocks, 104 p. Gulf of Maine Aquarium, PO Box 7549, Portland, ME 04112.

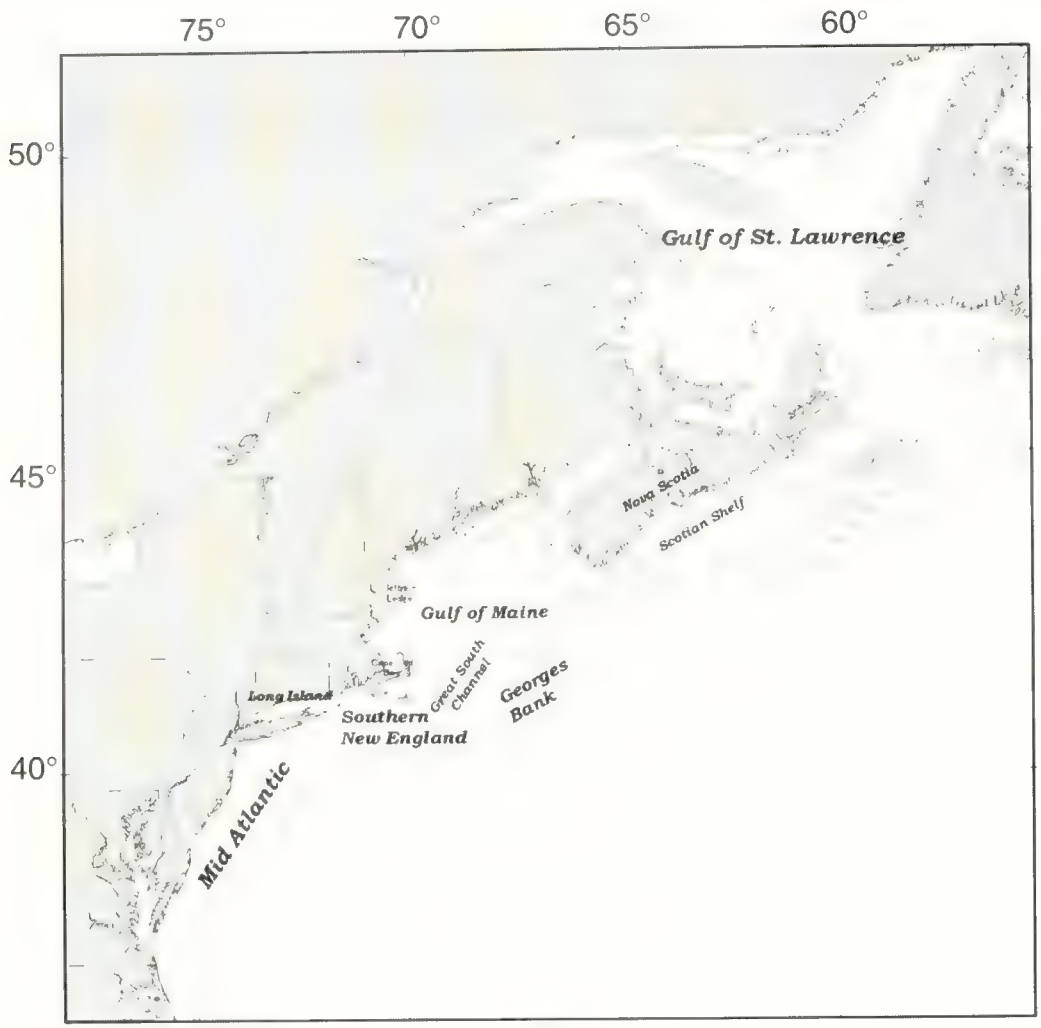


Figure 1

Regional map of the Mid-Atlantic, New England, and Canada area showing states, the providence of Nova Scotia, offshore place names, and the 100-m depth contour.

Shoals region during 1979–84 (Lough et al., 1985; Smith and Morse, 1993).

Presently pelagic fishes such as Atlantic herring and mackerel (*Scomber scombrus*) have recovered to historic high abundances (Clark, 1998). Atlantic herring have recovered to pre-1960s biomass and abundance and are now becoming the subject of renewed interest by fleets from the United States and Canada (Clark, 1998; NEFSC[2]). During a recent survey (spring 1999), herring were caught in 47% of the standardized tows and represented one of the top five species in terms of abundance and biomass (NEFSC[3]).

The presence and increase of spawning fish and larvae in historically important areas of Nantucket Shoals (Great South Channel area), Georges Bank, and along the coast of Maine have been documented ((Zinkevich, 1967; Stephenson and Kornfield, 1990; Smith and Morse, 1993; Stevenson[4]).

The purpose of this paper is to describe the magnitude of the decline and recovery of the herring complex in the Gulf of Maine–Georges Bank region and the chronology of

[2] NEFSC (Northeast Fisheries Science Center). 1998. Atlantic herring: report of the 27th Northeast regional stock assessment workshop (27th SAW). Stock Assessment Review Committee (SARC) consensus summary of assessments, 27 p. Northeast Fisheries Science Center, Woods Hole, MA 02543.

[3] NEFSC (Northeast Fisheries Science Center). 1999. Fisherman's report: bottom trawl survey. Woods Hole Laboratory, National Marine Fisheries Service, March 1–April 22, 1999, 20 p. Northeast Fisheries Science Center, Woods Hole, MA 02543.

[4] Stevensen, D. K. 1989. Spawning locations and times for Atlantic herring on the Maine Coast. Maine Department of Marine Resources Research Reference Document 89/5, 24 p. Maine Department of Marine Resources, Boothbay Harbor, ME 04575.

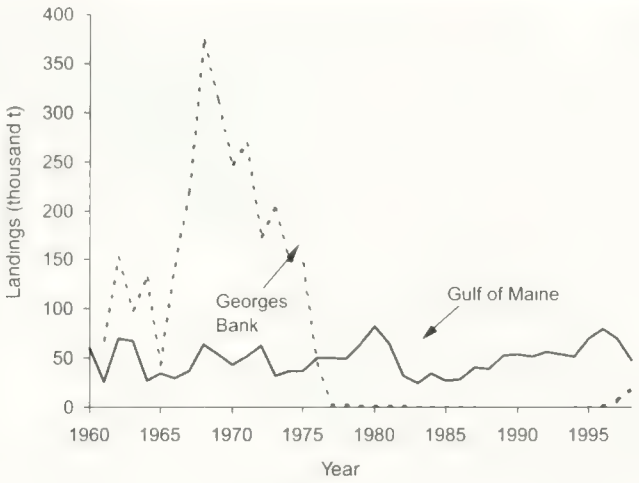


Figure 2

Landings of Atlantic herring (thousands of t) from the Gulf of Maine and Georges Bank, 1960–98.

the differential recovery by area by using NEFSC bottom trawl data from 1963 to 1998. We also wanted to examine two theories regarding the recovery of Georges Bank herring: 1) that it was due to a resurgence of extant spawners (Stephenson and Kornfield, 1990) or 2) that is was due to recolonization from adjacent components of the complex (Smith and Morse, 1993).

Methods

Details of the statistical design, areal coverage, standardization methods, gear type, and species catchability in the NEFSC bottom trawl surveys are provided in Grosslein (1969); Azarovitz (1981); Byrne et al. (1981), and a NEFSC report (NEFSC, 1988). Briefly, the surveys are based on a stratified random research design that covers the region from Cape Hatteras to the Scotian Shelf at depths between 27 and 200 m (15 to >100 fathoms), each spring and autumn.

We used data from spring (1968–98) and autumn (1963–98) bottom trawl surveys to produce indices of abundance, and plot distribution patterns for the Gulf of Maine–Georges Bank Atlantic herring complex. For spring, we used the same strata set (strata 1–30, 33–40, and 61–76) (Fig. 3) as used in the assessment of the herring complex (NEFSC[2]). We produced indices of total abundance (swept area numbers [millions]) to follow changes in the stock complex over time, assuming that a standardized survey tow covers 0.1 nmi and that all herring are available to the gear.

For autumn we used a smaller strata set (1–30, 33–40) (Fig. 3) to generate indices of abundance (area-swept numbers) because herring are seldom found south and west of Long Island during this season (NEFSC[2]). Changes in abundance by subregion (reflecting abundance trends by spawning components) were assessed by using indices for the Gulf of Maine (strata 26–28, 37–40), Nantucket Shoals (Great South Channel area) (strata 9–11, 23–25), and Georges Bank (strata 13–14, 16–17, 19–22, 29–30) (Fig. 3).

We produced box plots that represent the median survey catch location aggregated over a latitudinal gradient (35–45°N latitude) collapsed over the entire east-west longitude of the region. We repeated the same procedure for the longitudinal gradient (64–76°W longitude). These plots show the median, inter quartiles (25% and 75%), whiskers (1.5 times the absolute value of the interquartile range) and outliers of the data. We also constructed maps of spring survey catch locations for 1970, 1975, 1980, 1985, 1990, and 1995 to show trends in herring distribution and abundance over the time period. Changes in distribution and abundance during autumn 1963–98 are depicted in plots of Atlantic herring catch locations for 1965, 1970, 1975, 1980, 1985, 1990, and 1995.

We also produced box plots of bottom temperature for the sites where herring were captured during both seasons. For spring and autumn, we also plotted the proportion of survey tows with catches of Atlantic herring as a measure of how often surveys encountered Atlantic herring over the time series. We used LOWESS (locally weighted regression smoothing) (Cleveland, 1979) to make the temporal trends in both of these time series easier to follow.

Results

Atlantic herring abundance indices from spring surveys changed markedly during 1968–98 (Fig. 4A). A period of relatively high abundance (area swept, millions of fish), in

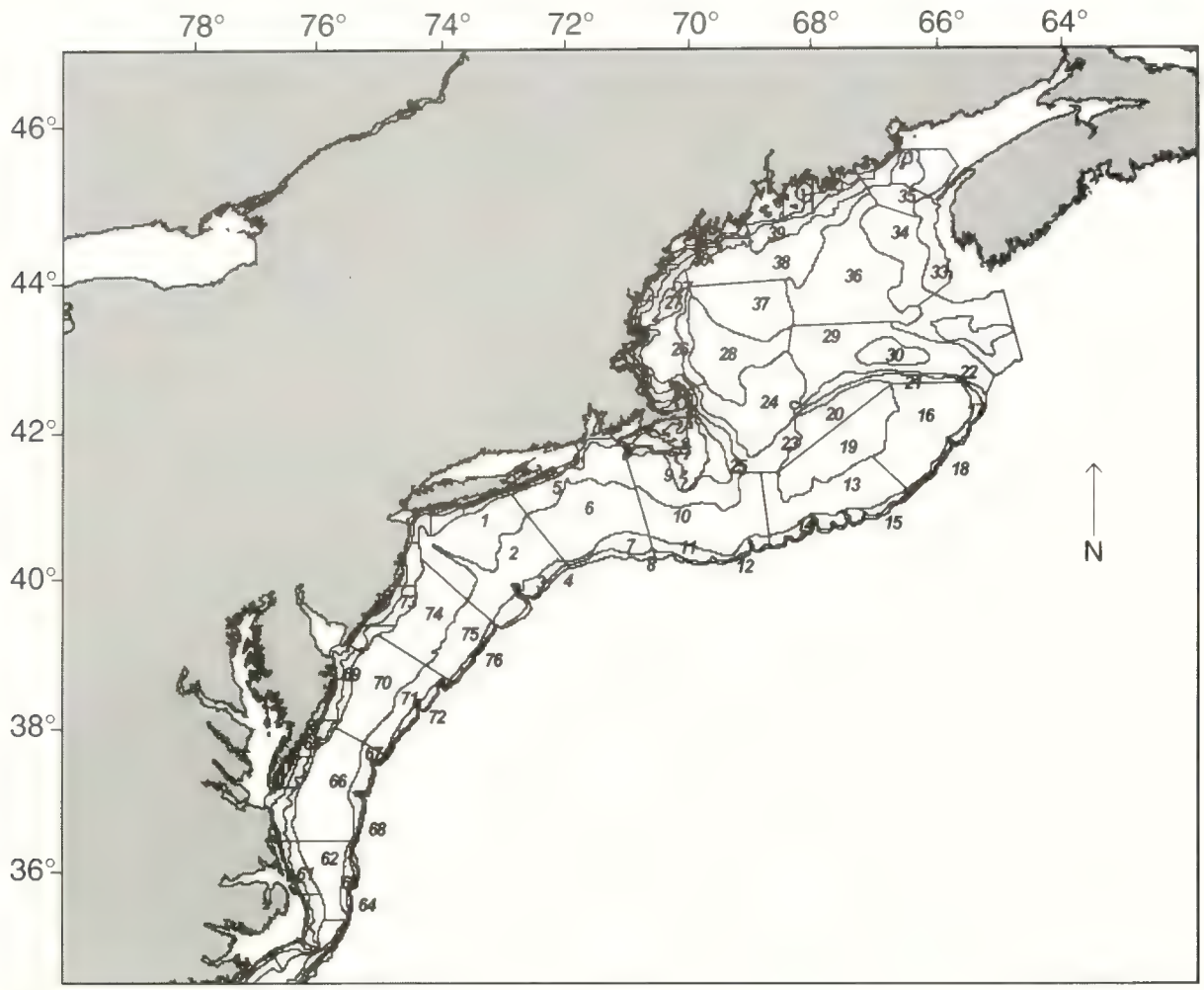


Figure 3

Survey strata used in the Northeast Fisheries Science Center research bottom trawl surveys for the region from Cape Hatteras, NC, to Nova Scotia, Canada.

the late 1960s was followed by a low abundance from 1971 to 1985. After 1985, abundance indices increased steadily to values that were 2–3 times larger (1993, 1996–98) than those at the beginning of the time series (Fig. 4A). Atlantic herring abundance was six times higher during 1992–98 than during 1968–75.

Herring spawn between mid-September and mid-October, and the timing is dependent on location and year. The NEFSC autumn research survey is usually conducted just after the spawning season for Atlantic herring, but this survey is a useful indicator of the abundance of spawners in the various component areas. Herring abundance in the autumn surveys was low (range 2.5–17.7 million fish) during 1963–67, very low from 1968–1986 (range 0.0–4.4 million fish), and much higher since 1987 (range 45.6–604.2 million fish) (Fig. 4B).

The herring complex occupied a consistently wider latitudinal range in the spring during the late 1980s and 1990s than in prior years. The complex was centered between 39°–41°N latitude during 1968–70 and then gradually shifted northwards (Fig. 5A). During 1982–84, the median latitude of the complex had moved north to 42° (north of Cape Cod); by 1984, the distribution of the stock complex was confined between 40°30′–44°10′N latitude, about a 50% decrease in latitudinal range as compared to 1968 (Fig. 5A). As abundance increased in the late 1980s, the center of the spring distribution of Atlantic herring moved southwards and the range extended; since 1989 the medial latitudinal position of the complex has remained at 41°N (Fig. 5A)

Major shifts in the longitudinal position of the complex have also occurred. During 1968–70, herring were generally west of 70°W longitude (Fig. 5B). Subsequently (through 1986) the complex shifted farther to the east. As abundance increased, in the late 1980s, the longitudinal center of the complex moved westward remaining at about 70°W longitude during 1989–98. During this time period, the east-west extent of the complex expanded greatly (Fig. 5B).

The median, interquartile range, and overall range in latitude of the herring complex in autumn is character-

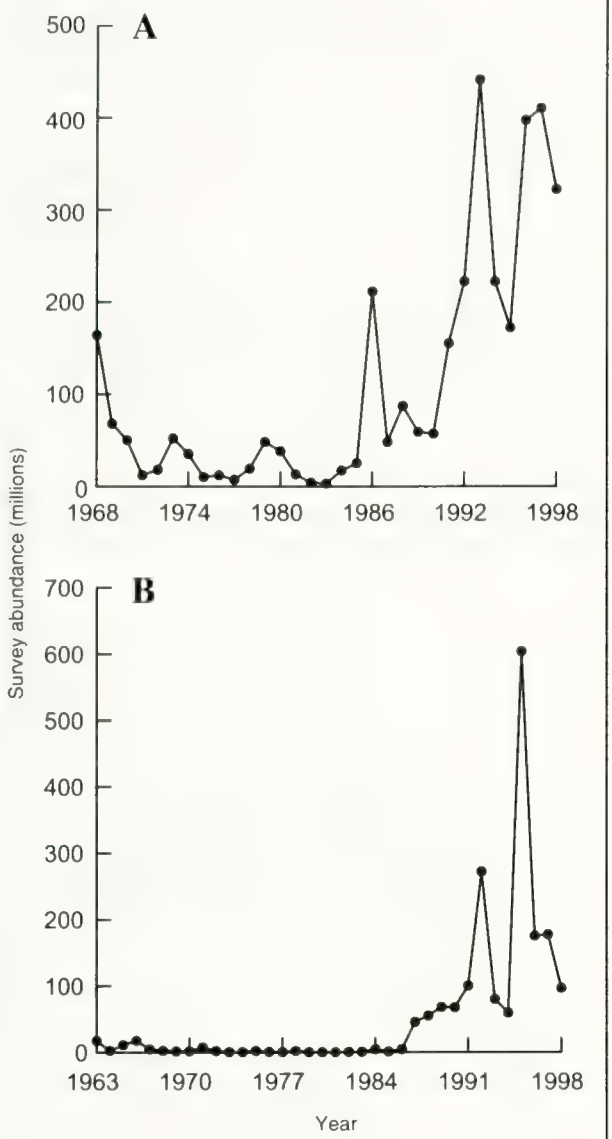


Figure 4

Abundance indices (swept area, millions of fish) of Atlantic herring from (**A**) spring bottom trawl surveys during 1968–98 and (**B**) autumn bottom trawl surveys during 1963–98.

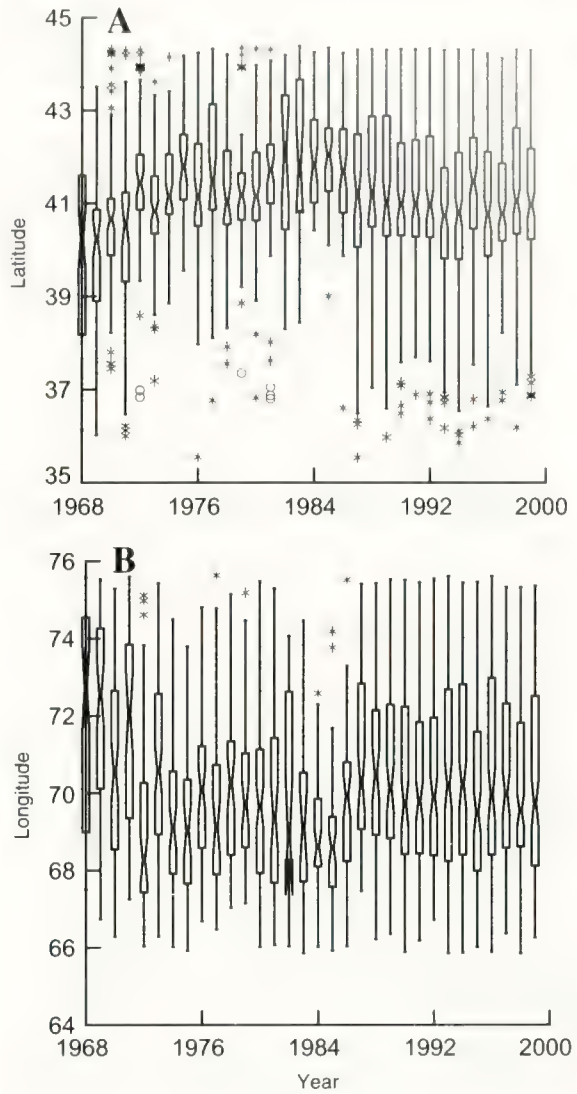


Figure 5

Median (notch), interquartile range, whiskers (±1.5 times the absolute value of the interquartile range), values outside the whiskers (*), and far outside the whiskers (o) of the (**A**) latitude and (**B**) longitude of positive catches of Atlantic herring from the spring NEFSC bottom trawl survey during 1968–98.

ized by rapid changes and a general movement to the north during 1963–75 (Fig. 6A). During 1963–64, the stock complex was centered around 42°, moved a full degree to the south by 1967, and then shifted north to almost 43° by 1975. Survey abundance was so low during 1976–81 that any trends in median latitude were obscured (Fig. 6A). As the stock recovered, median latitude became stable, ranging between about 42°00′ and 42°30′.

The median longitude of the complex hovered around 68°15′–68°45′ during 1963–72, then shifted to the west of 69° during 1973–86 (Fig. 6B). When recovery began, the median longitude of the complex moved slightly to the east of 69°, stabilized between 69°30′ and 69°50′ during 1991–95, and moved farther east during 1996–98 to about 68°35′ (Fig. 6B).

Since 1968, median bottom water temperatures for the entire continental shelf during spring have fluctuated between 5° and 7.5°C, with individual bottom locations ranging between 1° and 14°C and a few values falling outside this range (NMFS[5]). Herring maintained their pref-

[5] NMFS (National Marine Fisheries Service). 2001. Unpubl. data. Northeast Fisheries Science Center, Woods Hole, MA 02543.

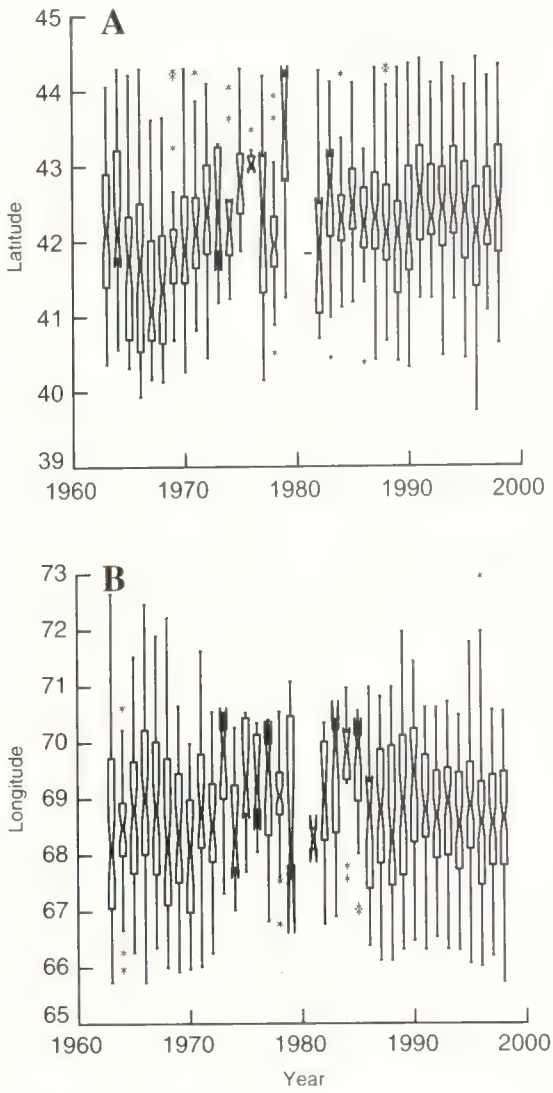


Figure 6

Median (notch), interquartile range, whiskers (±1.5 times the absolute value of the interquartile range), values outside the whiskers (*), and far outside the whiskers (o) of the (**A**) latitude and (**B**) longitude of positive catches of Atlantic herring from the autumn NEFSC bottom trawl survey during 1963–98.

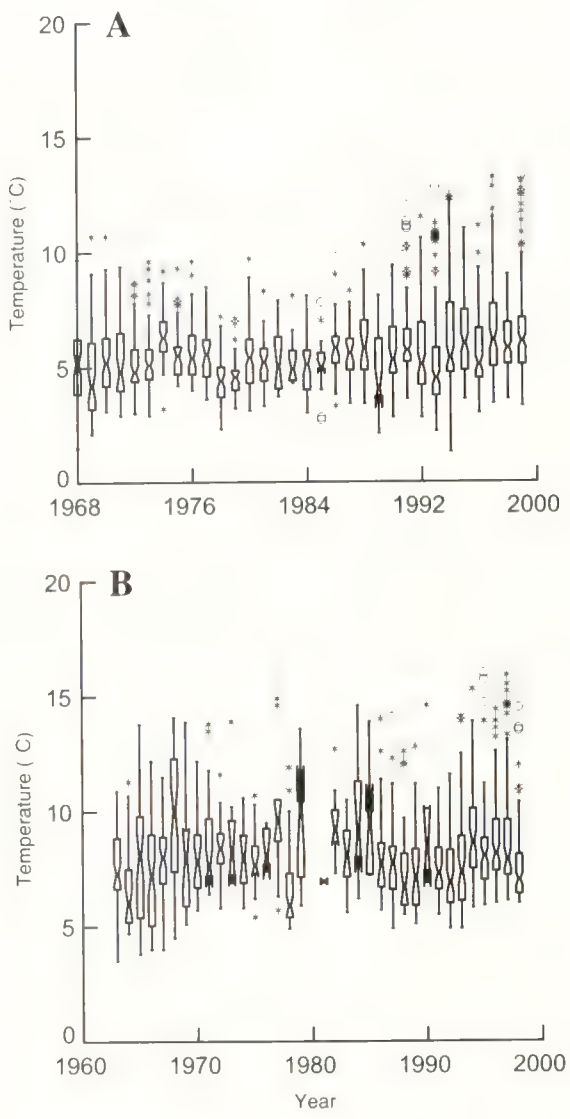


Figure 7

Median (notch), interquartile range, whiskers (±1.5 times the absolute value of the interquartile range), values outside the whiskers (*), and far outside the whiskers (o), of the bottom temperature of positive catches of Atlantic herring from the (**A**) spring NEFSC bottom trawl survey during 1968–98 and (**B**) autumn NEFSC bottom trawl survey during 1963–98.

erence for water temperatures that were cooler than the annual shelf-wide ranges; most herring were caught at bottom temperatures around 5°C during 1968–94 and at about 6°C thereafter (Fig. 7A). During 1972–91, the interquartile range in capture temperature was very narrow, about 1–2°C, expanding afterwards to 2–3°C (Fig. 7A). The overall range in capture temperatures increased greatly in the 1990s.

The median bottom water temperature for the continental shelf during autumn 1963–98 fluctuated between 8° and 12°C, and ranged between 3° and 25°C with a few higher observations (NMFS[5]). Herring were generally captured in the autumn surveys at bottom water temperatures around 8°C during 1963–76 and at about 7–8°C from 1983 to 1998 (Fig. 7B). The interquartile range in capture temperature was about 2–4°C (Fig. 7B), again much cooler than the shelf-wide ranges.

The proportional number of locations where Atlantic herring were captured during spring surveys declined

from 0.30 in 1968 to 0.09 in 1982 (Fig. 8A). During 1983–93, herring were captured in an increasing proportion of survey hauls; by the 1990s, the herring proportion in all survey tows was over 0.60 (Fig. 8A). Autumn surveys during the 1960s and 1970s also showed a declining trend in the proportion of stations containing herring. This decline was even more pronounced than in spring, with the proportion of herring at less than 0.05 of the sample sites during 1979–81 (Fig. 8B). This trend began to change in 1982 and by the 1990s the proportion of tows with herring was well over 0.40 (Fig. 8B).

Spring distribution maps from selected years (1970–95) show that significant changes in herring distribution occurred during 1968–98. In 1970 herring were encountered at 74 sites in the central Gulf of Maine (GOM), on southern Georges Bank (GB), and across the continental shelf from south of Nantucket to Chesapeake Bay (Fig. 9). During 1975, fewer sampling locations (39 sites) had herring and the distribution was constricted. The complex was confined to a few areas in the central GOM, on southern GB, south of Cape Cod, and off of Long Island (Fig. 9). In 1980, fish were encountered (89 sites) along eastern GB and found across western-southern GB to south of Long Island. During 1985, the spring distribution (48 sites) was more restricted than in 1980. By 1990 Atlantic herring were found at 101 sites throughout the GOM, western and southern GB, and across the shelf from Cape Cod to Chesapeake Bay. In 1995, herring were even more widely dispersed (108 sites) across the continental shelf.

Abundance of herring from these selected spring research survey years reflect the general decline in the stock in the late 1970s and recovery to much higher levels in the late 1990s (Fig. 9). In 1970, herring were abundant over the entire continental shelf from Nantucket to Chesapeake Bay with the highest abundance off Long Island and New Jersey (Fig. 9). During the late 1970s, through the mid 1980s, herring were less abundant and the largest catches (101–500 fish per station) were generally taken south of Cape Cod (Fig. 9). By the 1990s, herring were abundant over a wider area and catches in the 101–500 fish-per-tow range were common.

Maps of autumn survey catch locations depict significant spatial changes in herring distribution during the past 30 years (Fig. 10). In 1965 postspawning fish were located (47 sites) in the central GOM, on Jeffreys Ledge, Nantucket Shoals, and the shelf-slope break along western to northern GB (Fig. 10). In 1970 herring were caught at 25 sites (mostly in the GOM and on eastern GB), in 1975 at only 18 sites, and in 1980 at only one location (along the coast of Maine). The number of capture sites increased in 1985 (17) when herring were found primarily in the Stellwagen Bank-Jeffreys Ledge region, and at a few sites on Georges Bank (Fig. 10). In 1990, herring were widely dispersed (31 sites) along the coast of Maine, Jeffreys Ledge, and Nantucket shoals, and in 1995 herring were dispersed throughout the entire region (75 sites) (Fig. 10).

In the early part of the autumn survey time series, herring were widely dispersed, but not very abundant. In 1965, only a few tows had catches greater than 50 fish (Fig. 10). During 1970–85 very few herring were taken and most tows represented only single fish (Fig. 10). By 1990 a general recovery was apparent and catches of 50+ fish per station were common. Atlantic herring were again abundant along the coast of Maine, on Jeffreys Ledge, and in the Great South Channel area (Fig.10). In 1995, herring were abundant over the entire Gulf of Maine–Georges Bank region.

Survey abundance indices of herring in the Gulf of Maine, on Nantucket Shoals, and on Georges Bank, increased greatly since the mid 1980s, but at different rates (Fig.11). Increases in the GOM (range 2.8–85.9 million fish, 1987–98) and GB (range 2.1–120 million fish, 1991–98) regions appeared to be about equal in magnitude although the recovery in the GOM began earlier than on GB (Fig.

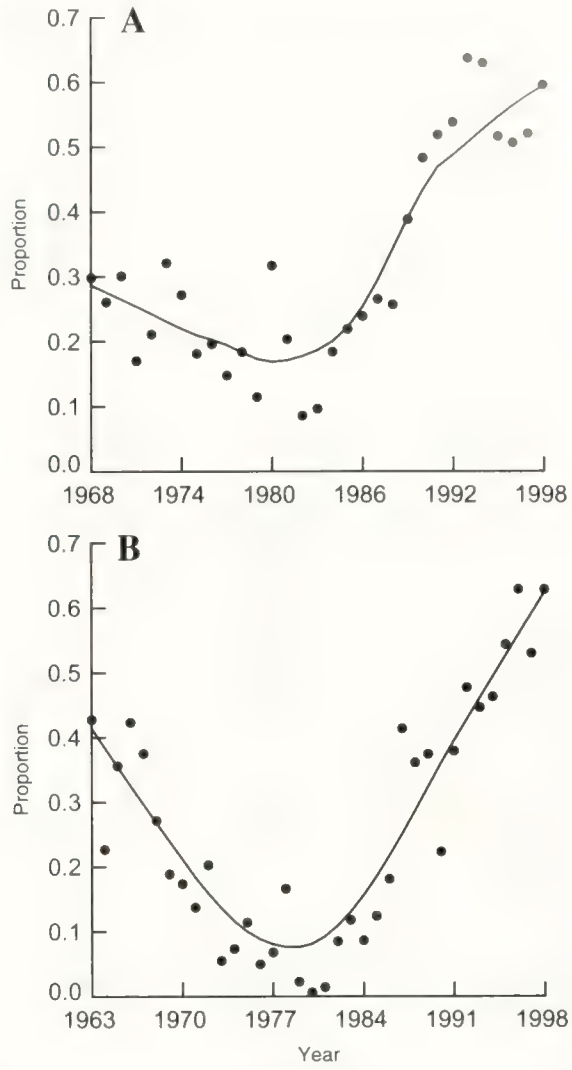


Figure 8

Proportion of survey tows with positive occurrences of Atlantic herring with a LOWESS curve for the data from (**A**) spring bottom trawl surveys during 1968–98 and (**B**) autumn bottom trawl surveys during 1963–98.

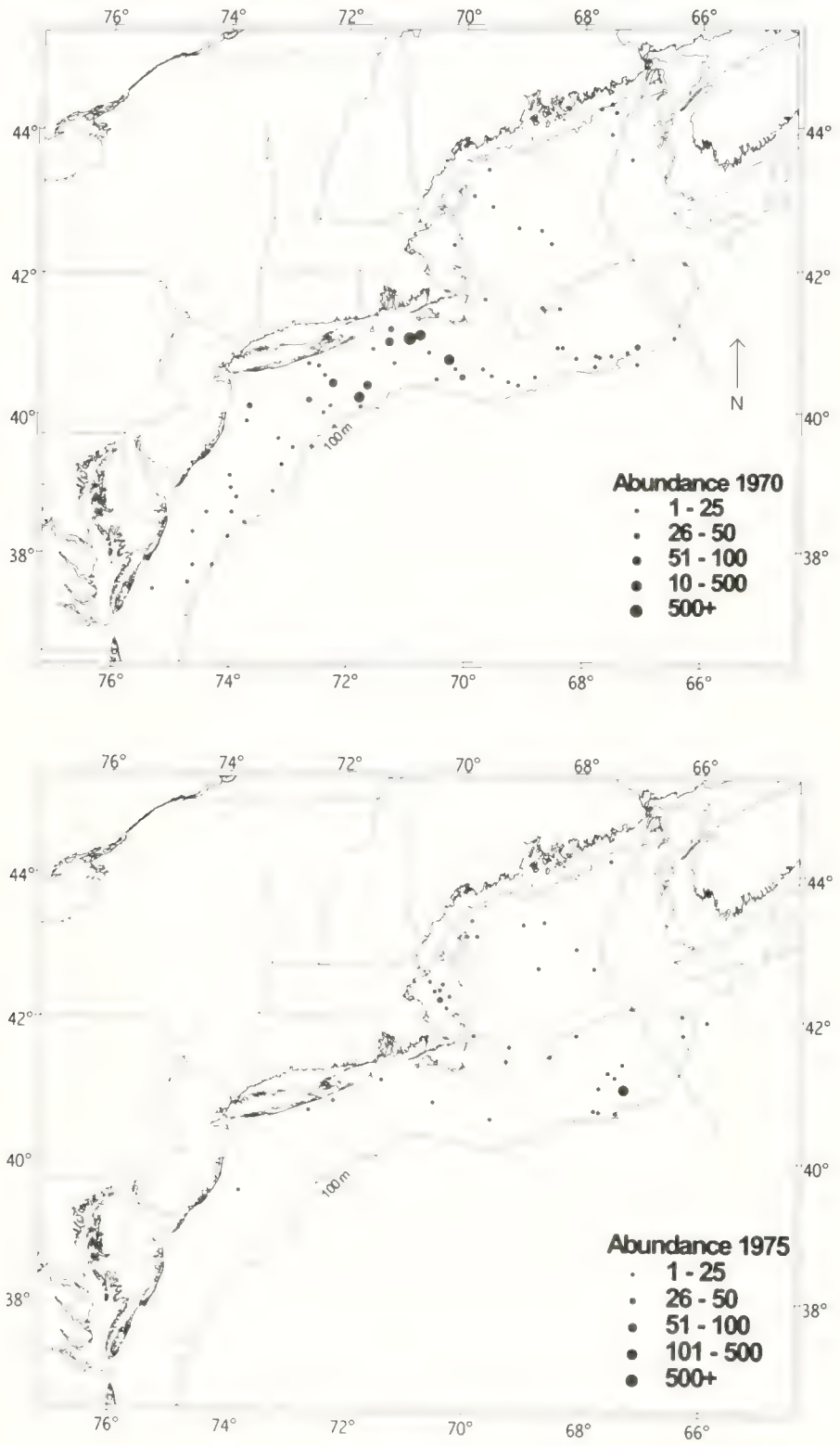
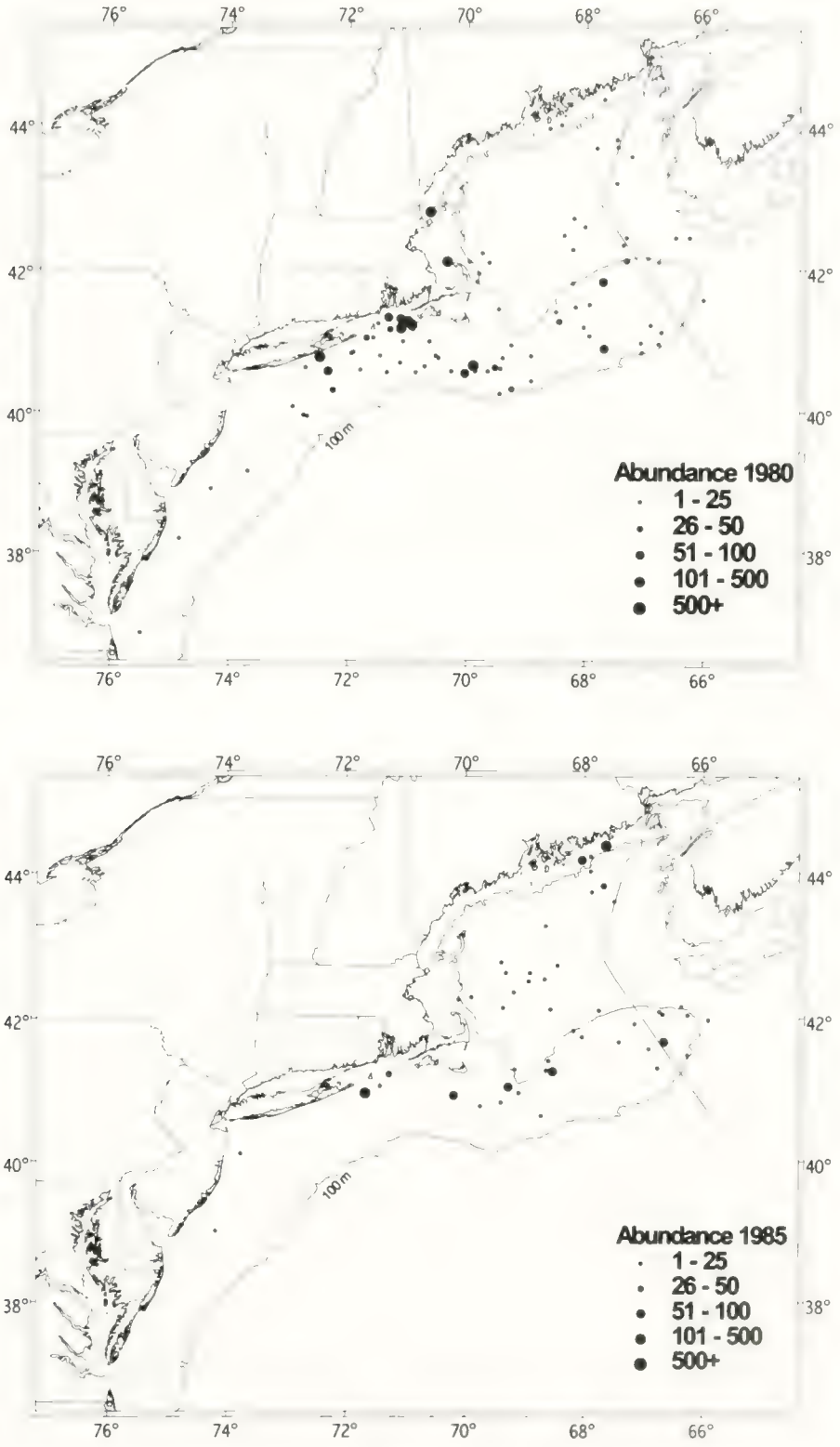


Figure 9

Catch locations and abundance (number of fish per station) for Atlantic herring for selected years (1970, 1975, 1980, 1985, 1990, 1995) from spring bottom trawl surveys conducted during 1968–98.



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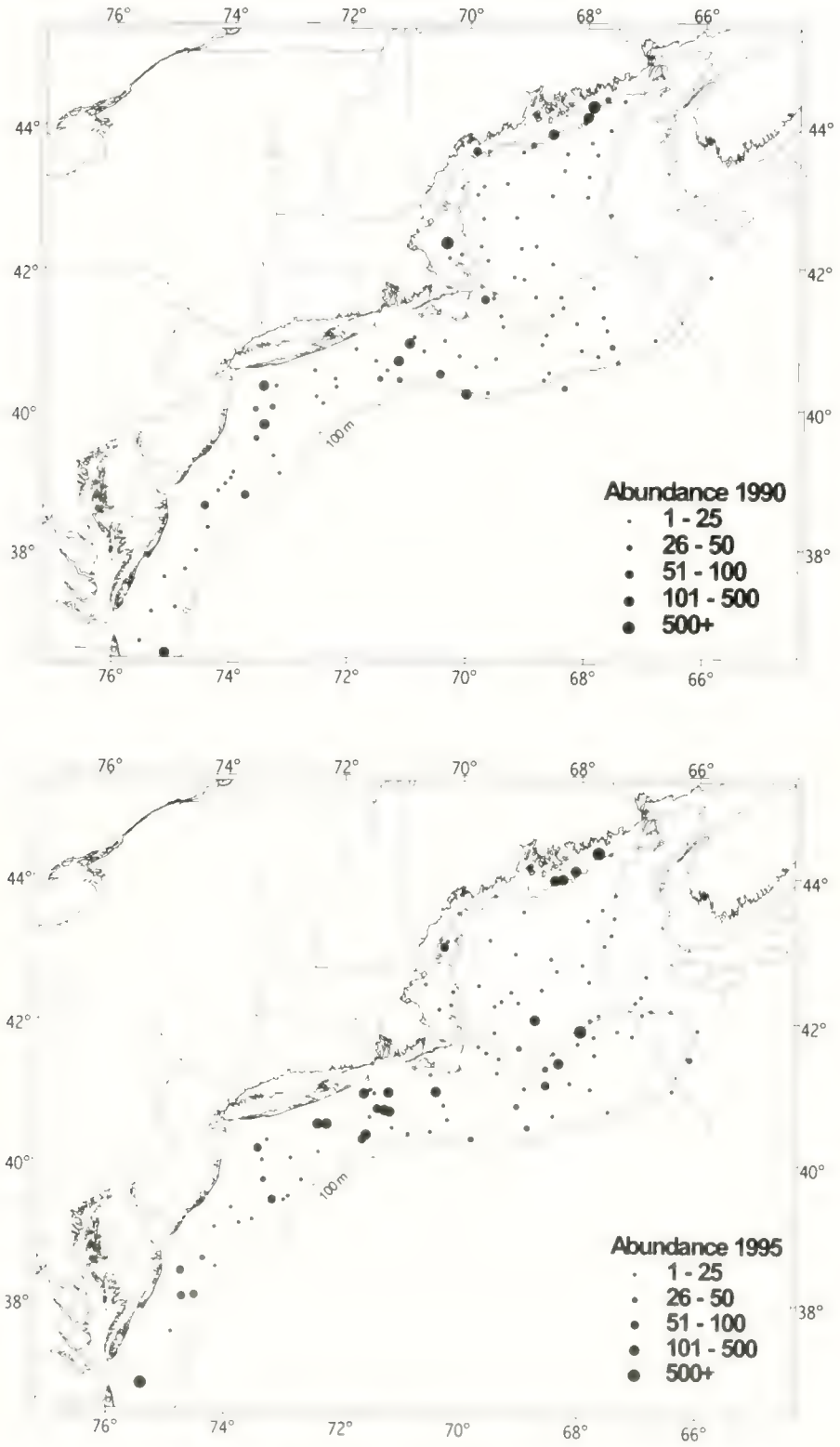

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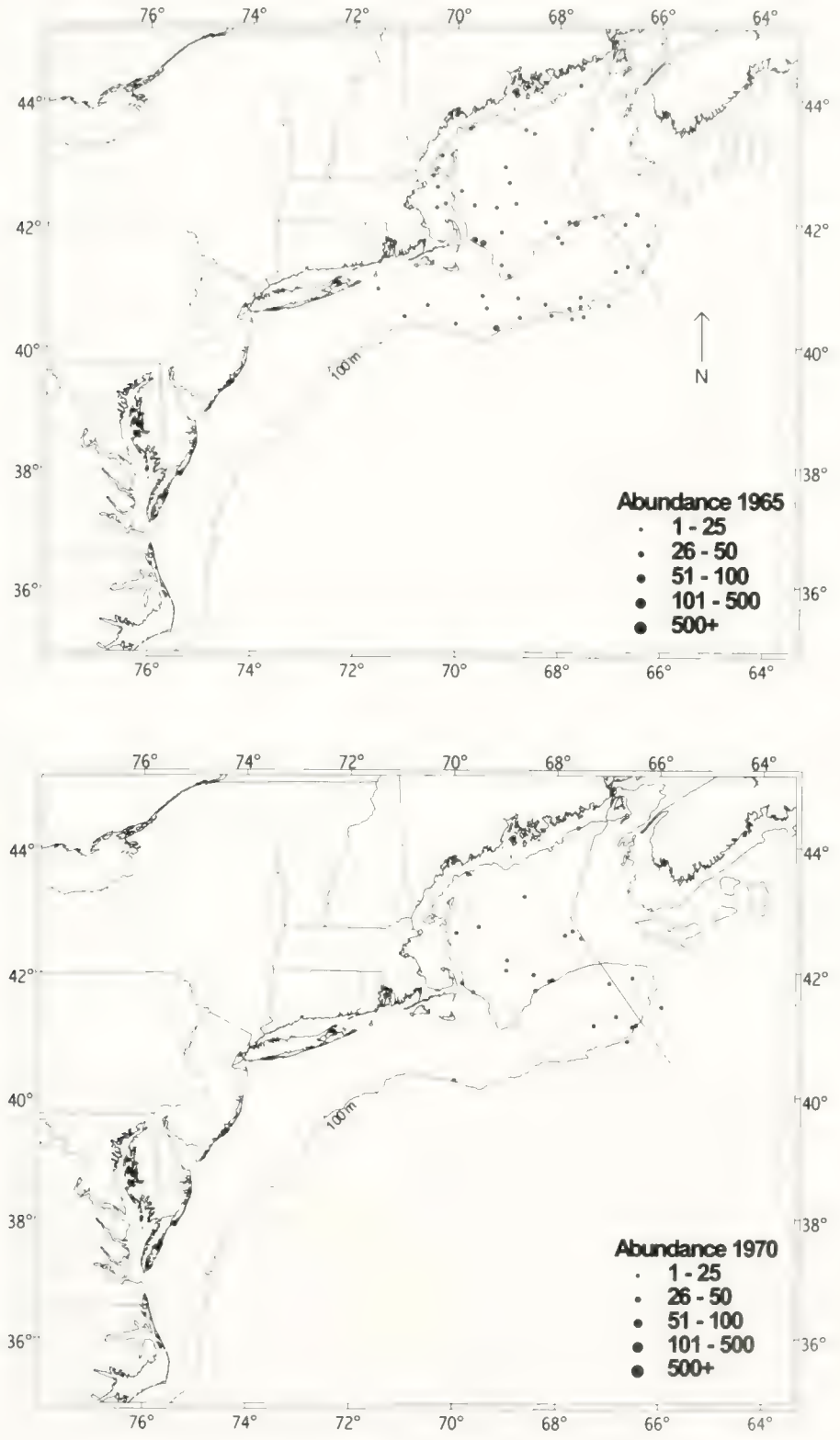


Figure 10

Catch locations and abundance (number of fish per station) for Atlantic herring for selected years (1965, 1970, 1975, 1980, 1985, 1990, 1995) from autumn bottom trawl surveys conducted during 1963–98.

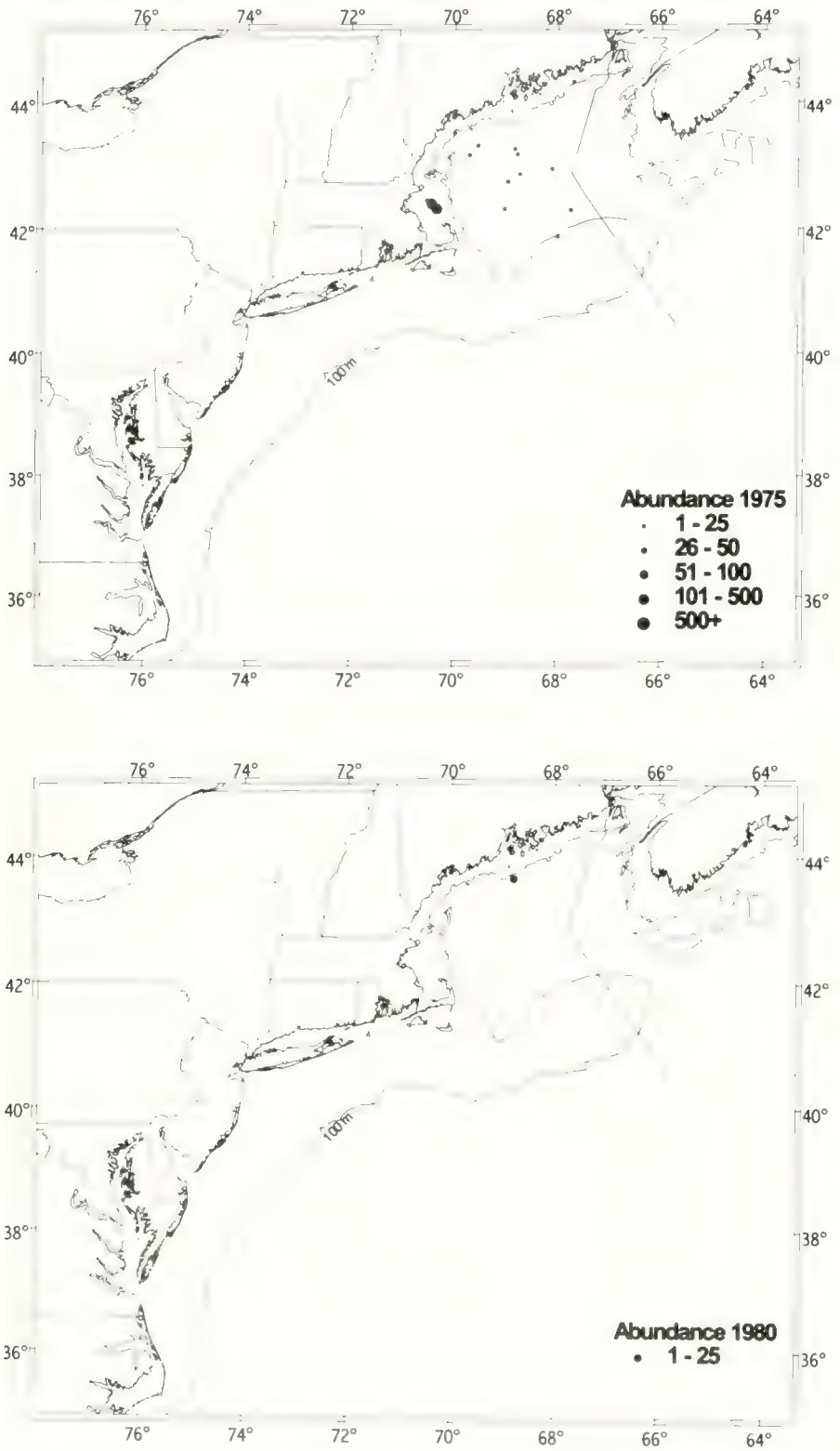
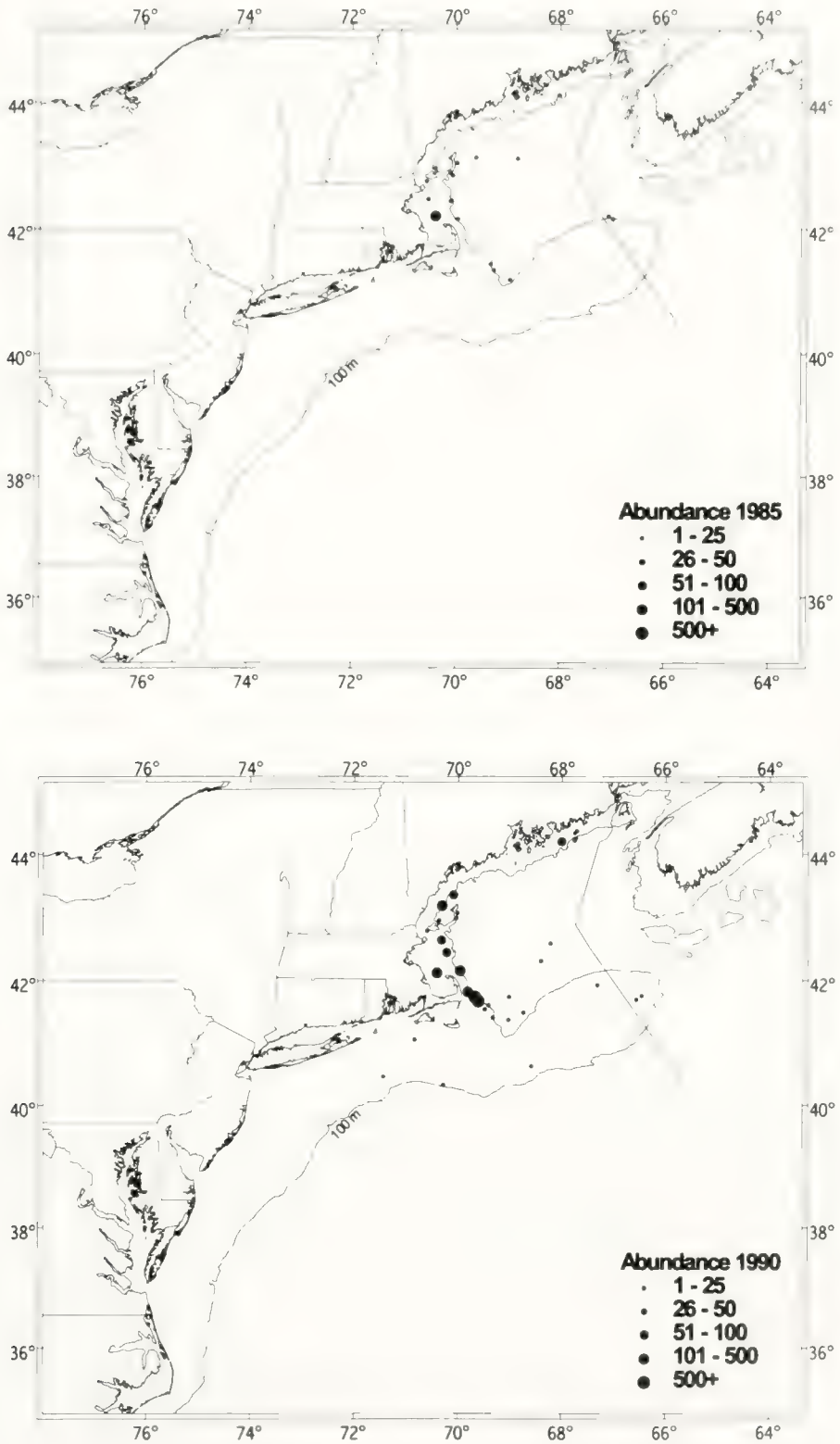


Figure 10 (continued)



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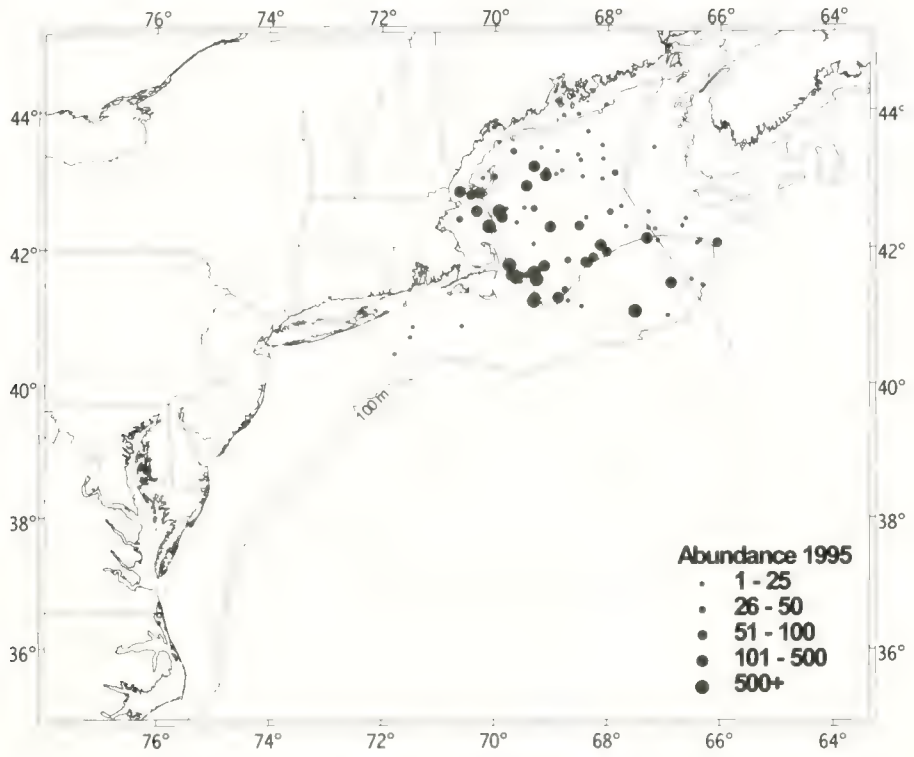

Figure 10 (continued)

11). The recovery in the Gulf of Maine started in 1984 and continued through to 1998 (Fig. 11A). The largest overall increase in abundance has occurred in the Nantucket Shoals region (range 28.8–398.3 million fish) (Fig. 11B). Similarly, after a long hiatus from 1963–1986, this stock component increased considerably during 1987–98. The Georges Bank component was the last to recover, with significant increases in abundance beginning in 1992 (Fig. 11C).

Discussion

Atlantic herring are currently abundant in the Gulf of Maine–Georges Bank region as evidenced by research survey results and recent stock assessments (NEFSC[2]). This resource was heavily exploited during 1961–76 by distant-water fishing vessels with catches that were not sustainable, resulting in the collapse of the Georges Bank component in 1977. The causes of this collapse have been ascribed to excessive fishing mortality and concentration of effort on spawning areas (Anthony and Waring, 1980). ICNAF routinely set total allowable catches (TACs) in excess of scientific recommendations and these TACs were often exceeded (Anthony and Waring, 1980). Spawning concentrations were heavily fished, and egg and larval production declined steadily, followed by the complete absence of larvae on Georges Bank for an entire decade (Anthony and Waring, 1980; Lough et al., 1985; Smith and Morse, 1993).

Full recovery of the Atlantic herring resource has required almost two decades (NEFSC[2]). Spawning area closures and restrictions in the Gulf of Maine beginning in the 1980s may have been influential, but the relative impact of these indirect measures cannot be assessed (Stevenson[4]). During 1978–94 there were almost no offshore landings and abundance and biomass for the GB component improved steadily (NEFSC[2]).

The distribution range of the herring complex was greatly reduced after each of the three stock components were heavily fished; the extent of the spring distribution was much reduced by the early 1980s and autumn spawning activity was confined to the western Gulf of Maine. The relative encounter rate in both research surveys, as measured by the proportion of tows with herring, also declined during this period. As the complex began to recover, its range extended and the proportion of survey tows with herring increased dramatically. The complex was more widely dispersed by the mid 1990s with the recovery of all three components to, or above, historic abundance and biomass (NEFSC[2]).

Murawski (1993) found that temperature is a very important factor in determining the distribution of pelagic fishes, particularly Atlantic herring. Herring appear to have maintained a preferred thermal regime despite elevated and variable overall shelf temperatures in spring and autumn, and large changes in abundance. The ±5°C median spring temperature for 1968–94 from our study is in agreement with the average of 4.8°C from Murawski (1993). After the complex recovered, the median spring bottom temperature increased slightly to about 6°, probably indicative of the much broader range of the complex. Murawski (1993) calculated an autumn average of 8.5° for Atlantic herring and the median from the current study was 7–8°. This autumn preference reflects the distribu-

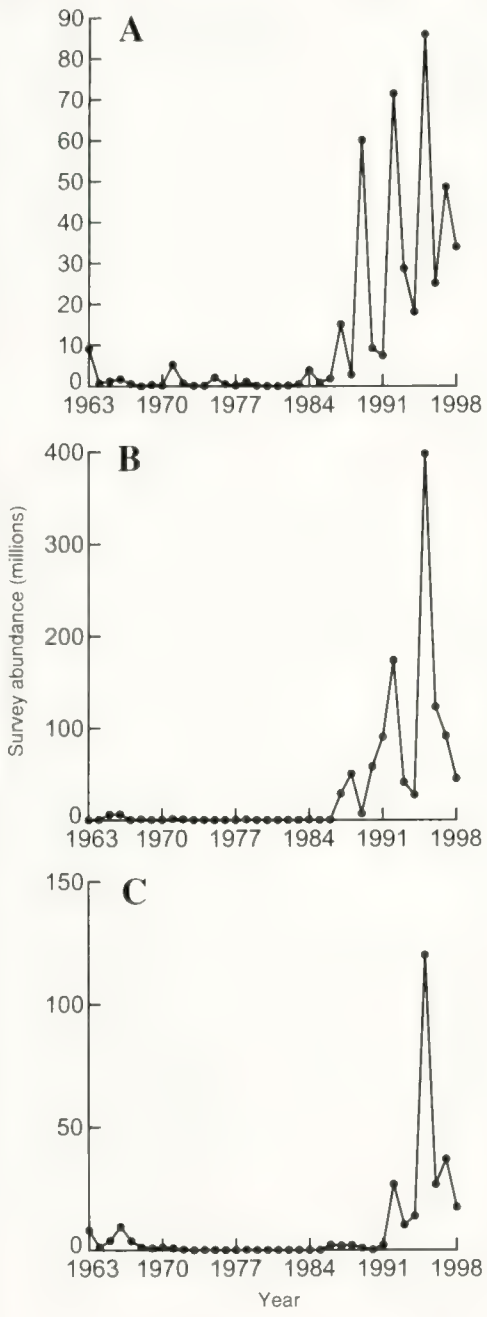

Figure 11

Abundance (swept area, millions of fish) of Atlantic herring from (**A**) the Gulf of Maine, (**B**) Nantucket Shoals, and (**C**) Georges Bank from autumn bottom trawl surveys during 1963–98.

tion of postspawning fish in the cooler waters of the Gulf of Maine and Northern Georges Bank. Although thermal conditions play a major role in the zoogeography of fishes, the influence of abundance was probably overwhelming in producing the recovery of the historic range in distribution observed in the Atlantic herring complex.

Several independent sources of information suggest that the recovery of this stock occurred in a stepwise manner with the Gulf of Maine component recovering first, followed by the Nantucket Shoals component, and finally the Georges Bank component. The autumn bottom trawl survey data showed an improved trend in the Gulf of Maine in 1984, the Nantucket Shoals component in 1987, and Georges Bank in 1992. Larval surveys conducted during 1971–90 showed a progression of larval abundance from the Cape Cod Bay-Stellwagen Bank area in 1976–84, to Nantucket Shoals in 1985–87, and on Georges Bank in 1988–90 (Smith and Morse, 1993). Larval distribution data suggested that larvae from Jeffreys Ledge spawners were probably transported to Nantucket Shoals and that in subsequent years larvae from these areas were transported or adults moved to western Georges Bank and finally eastern Georges Bank (Smith and Morse, 1993). The general pattern of water circulation in the region (McGillicuddy et. al., 1988) also favors this hypothesis for the recovery.

Smith and Morse (1993) suggested that the larval survey data support the hypothesis that a recolonization of Atlantic herring occurred on Nantucket Shoals and Georges Bank. The data from their study showed a chronological pattern in larval abundance and distribution, beginning in the Gulf of Maine and progressing toward the Nantucket shoals region and finally to Georges Bank. In contrast, Stephenson and Kornfield (1990) asserted that the reappearance of herring on Georges Bank was more related to a resurgence of low numbers of stock-specific endemic fish. The autumn NMFS bottom trawl survey data tend to support the conclusions of Smith and Morse (1993) in both direction and timing. Survey indices show a progressive recovery in herring abundance from the Gulf of Maine to Nantucket Shoals, and finally to Georges Bank.

Significant changes in stock distribution, shifts in centers of primary abundance, and regional declines or disappearance of historically important spawning contingents are evident from the data. Autumn indices show that the stock component in the Gulf of Maine reached very low abundances during 1973–83 and that the Nantucket Shoals and Georges Bank components were nearly, if not actually, extirpated. Recovery times for these two components of the stock were relatively long—on the order of 10–15 years. Without a local supply of larvae, recovery was delayed considerably. Recovery was probably contingent on a supply of larval herring from the Gulf of Maine that eventually recolonized the offshore areas. Spawning restrictions along the coast of Maine and on Jeffreys Ledge in the 1980s may also have contributed to the recovery of Gulf of Maine component, thereby setting in motion the recovery of the entire stock complex.

Acknowledgments

We thank the dedicated personnel from the Northeast Fisheries Science Center and the many volunteers who worked tirelessly to collect the bottom trawl survey data during 1963–98.

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Abstract—Age, size, abundance, and birthdate distributions were compared for larval Atlantic menhaden (*Brevoortia tyrannus*) collected weekly during their estuarine recruitment seasons in 1989–90, 1990–91, and 1992–93 in lower estuaries near Beaufort, North Carolina, and Tuckerton, New Jersey, to determine the source of these larvae. Larval recruitment in New Jersey extended for 9 months beginning in October but was discontinuous and was punctuated by periods of no catch that were associated with low water temperatures. In North Carolina, recruitment was continuous for 5–6 months beginning in November. Total yearly larval density in North Carolina was higher (15–39×) than in New Jersey for each of the 3 years. Larvae collected in North Carolina generally grew faster than larvae collected in New Jersey and were, on average, older and larger. Birthdate distributions (back-calculated from sagittal otolith ages) overlapped between sites and included many larvae that were spawned in winter. Early spawned (through October) larvae caught in the New Jersey estuary were probably spawned off New Jersey. Larvae spawned later (November–April) and collected in the same estuary were probably from south of Cape Hatteras because only there are winter water temperatures warm enough (≥16°C) to allow spawning and larval development. The percentage contribution of these late-spawned larvae from south of Cape Hatteras were an important, but variable fraction (10% in 1992–93 to 87% in 1989–90) of the total number of larvae recruited to this New Jersey estuary. Thus, this study provides evidence that some *B. tyrannus* spawned south of Cape Hatteras may reach New Jersey estuarine nurseries.

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Recruitment of larval Atlantic menhaden (*Brevoortia tyrannus*) to North Carolina and New Jersey estuaries: evidence for larval transport northward along the east coast of the United States*

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The larvae of some species of fishes that spawn in the South Atlantic Bight (SAB; Cape Hatteras, North Carolina to Cape Canaveral, Florida) are transported northward to the Middle Atlantic Bight (MAB; Cape Cod, Massachusetts to Cape Hatteras, North Carolina) where they eventually use estuaries as juvenile nurseries. Kendall and Walford (1979) first suggested that spring-spawned bluefish, *Pomatomus saltatrix*, from the SAB are transported several hundreds of kilometers northward where they eventually enter estuaries in the MAB (Hare and Cowen, 1996). Nyman and Conover (1988) and McBride and Conover (1991) used otolith analyses to confirm the presence of a spring-spawned component from the SAB in the juvenile bluefish population in MAB estuaries. The larvae of several other species from more southerly areas are also expatriated to the MAB (Hare and Cowen, 1991; Cowen et al., 1993; McBride and Able, 1998). Tropical and subtropical planktonic invertebrates are also known to occur in the MAB (Cox and Wiebe, 1979). Some seemingly unusual occurrences of Atlantic menhaden larvae in New Jersey during the winter suggested that the same pattern might occur for this species.

Atlantic menhaden, *Brevoortia tyrannus*, is a clupeid that migrates along the coast from the Gulf of Maine to Florida and adults spawn throughout this range. Studies (summarized in Warlen, 1994; Epifanio and Garvine, 2001) have shown that this species spawns off New England from late spring into summer and again in early fall, off the mid-Atlantic states in spring and fall, and in the SAB from October to March. Maximum numbers of Atlantic menhaden probably spawn during winter in offshore waters south of Cape Hatteras (Reintjes, 1969; Judy and Lewis, 1983) and North Carolina waters are likely one of the

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major spawning grounds (Higham and Nicholson, 1964). The larvae are recruited to estuaries in North Carolina (Lewis and Mann, 1971; Warlen and Burke, 1990; Hettler and Barker, 1993; Warlen, 1994). For the purposes of this article, we define estuarine recruitment as the ingress or immigration of larvae to the estuary from the ocean.

A variety of field and laboratory observations suggest that spawning is not likely to occur at the temperatures found from late fall through spring in the MAB. Field observations in Naragansett Bay, Rhode Island (Govoni[1]), have indicated that peak densities of Atlantic menhaden eggs are found at 18–20°C and very few eggs are found at temperatures below 16°C. Kendall and Reintjes (1975) found Atlantic menhaden eggs at only one of 92 stations during one (9 November–14 December) of three late fall-winter cruises in the MAB. A summary of the Marine Monitoring Assessment and Prediction (MARMAP) collections, for November–April of the 1979–87 surveys in the MAB west of longitude 72°W from Montauk Point, New York, to Cape Hatteras, North Carolina, showed late-stage eggs in only 25 of 2247 plankton hauls (Berrien and Sibunka, 1999). Except in one haul in January near Cape Hatteras, all other Atlantic menhaden eggs found in this MAB survey were collected in November. Atlantic menhaden eggs were collected in Onslow Bay, North Carolina, in December 1992 only at temperatures of 17–23.5°C, and most were found at about 22°C (Peters[2]). During South Atlantic recruitment experiment studies (SABRE), eggs were found between the Gulf Stream and mid-shelf fronts (17–23°C) in Onslow Bay (Checkley et al., 1999). Reduced temperatures (14.8–15.7°C) appeared to diminish the ability to induce spawning of Atlantic menhaden in the laboratory (Fitzhugh and Hettler, 1995) as compared to temperatures >17°C. Even if spawning can occur at temperatures <15°C, there must be successful hatching and larval development to ensure larval survival. At 16°C, early larval growth in dry weight was about one-half that at 20°C (Powell, 1993). Therefore, we concluded that optimum temperature for hatching and larval survival and growth is probably ≥16°C.

From the above findings, we concluded that late-fall to early-spring water temperatures in the MAB are unsuitably low for Atlantic menhaden spawning. Water temperatures in the MAB to at least 300 km offshore are usually 7–14°C from mid-November through April (Benway et al., 1993a, 1993b). However, Atlantic menhaden larvae, probably spawned during that period, recruit to New Jersey estuaries from winter to spring (Witting et al., 1999). These two facts suggest a warmer water (i.e. southern) origin of the wintertime larval Atlantic menhaden recruits in New Jersey and prompted us to ask whether larval transport from the SAB could explain this occurrence. To test this hypothesis, we examined synoptic collections of larval Atlantic menhaden recruiting to estuaries in North Carolina and in New Jersey from fall to spring. We determined the duration of recruitment, age and size, relative abundance, spawning season, and relative contribution of cohorts of larvae spawned in a given calendar week to the estuarine recruitment of Atlantic menhaden larvae to an estuary in each area. These data were used to estimate the percentage of larval Atlantic menhaden collected in the New Jersey estuary that may have originated in the SAB.

Methods

Larval occurrence and abundance

Sampling for larval Atlantic menhaden was conducted in North Carolina and New Jersey as these larvae recruited to the estuaries from the Atlantic Ocean. In North Carolina, larvae were collected at a station adjacent to Pivers Island in the lower Newport River estuary about 2 km inside Beaufort Inlet (Fig. 1). Nighttime sampling was conducted weekly at mid-flood tide during the expected recruitment period in three seasons (15 November 1989–2 May 1990, 14 November 1990–24 April 1991, and 19 November 1992–11 May 1993). Initial seasonal sampling was based on previous years' collections (Lewis and Mann, 1971; Warlen, 1994) that showed that Atlantic menhaden larval recruitment usually began no earlier than mid-November. End-of-year sampling terminated when larval density dropped to zero. Larvae were collected in four consecutive sets of a 1×2 m neuston net with 947-µm mesh fished (most sets 5–7 minutes long) just under the surface from a bridge platform. A flow meter was attached to the net to estimate the amount of water filtered. Details of the sampling protocol are given in Warlen (1994). Ichthyoplankton samples were preserved in 95% ethanol and diluted so that the final concentration was at least 70% ethanol. Catches were standardized as the number of larvae/100 m^3 of water filtered. The mean of the density data for the four net sets on a given night was used as the density estimate of Atlantic menhaden larvae recruiting during the flood tide.

In New Jersey, gear type and sampling effort were similar in concept but differed in some details (Witting et al., 1999). Ichthyoplankton were collected with a 1-m diameter (1-mm mesh) plankton net fitted with a flow meter. The net was fished during nighttime flood tides from a bridge spanning Little Sheepshead Creek about 3 km upstream from the mouth that is approximately 2.5 km inside Little Egg Inlet (Fig. 1). Water depth at this bridge and the Pivers Island bridge was approximately 4 m. Sampling was conducted over the same years as in North Carolina, and sampling was conducted year round in New Jersey. A mean larval density (number larvae/100 m^3 water fished) was calculated from all samples on each night (five surface and five bottom sets in 1989–90, three surface and three bottom sets in 1990–91, three mid-water sets in 1992–93) and was used to estimate Atlantic menhaden larval recruitment during the flood tide. Each net set lasted 0.5 hour. Current speeds were generally 25–50 cm/s,

[1] Govoni, J. J. 1996. Personal commun. Center for Coastal Fisheries and Habitat Research, National Ocean Service, NOAA, 101 Pivers Island Rd., Beaufort, NC 28516.

[2] Peters, D. S. 1996. Personal commun. Center for Coastal Fisheries and Habitat Research, National Ocean Service, NOAA, 101 Pivers Island Rd., Beaufort, NC 28516.

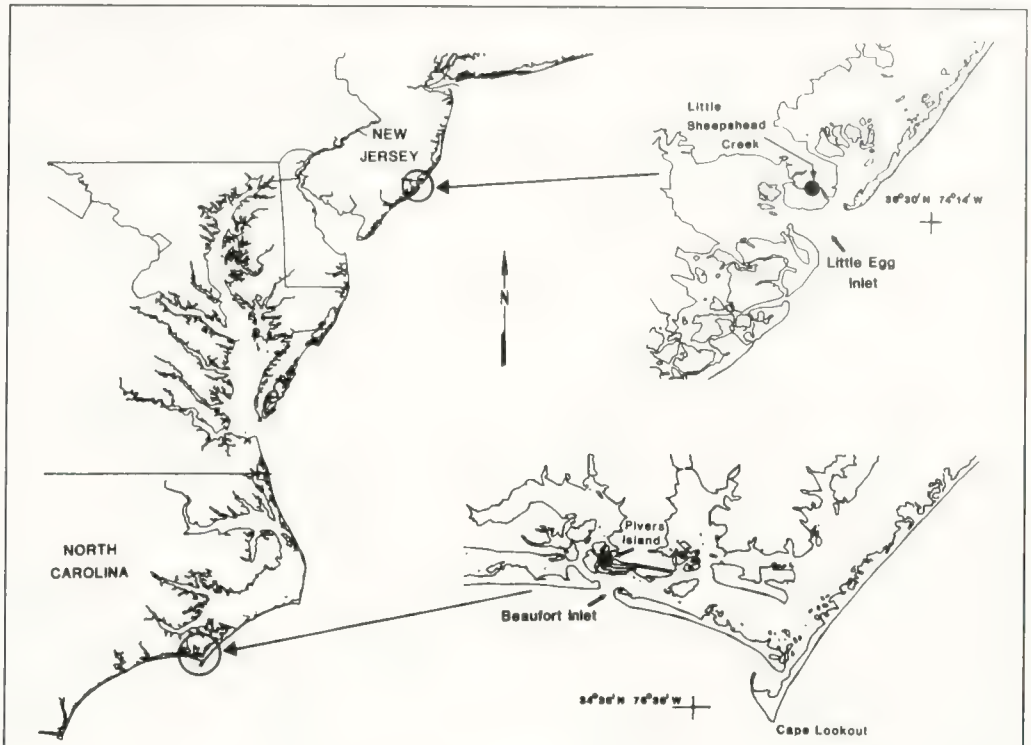

Figure 1

Location of sampling sites for larval Atlantic menhaden (*Brevoortia tyrannus*) collected at Little Sheepshead Creek, New Jersey, and Pivers Island, North Carolina, during 1989–90, 1990–91, and 1992–93.

and approximated those measured in North Carolina. As in North Carolina, samples were preserved in 95% ethanol.

We assumed that larval fish densities within and among years at a site were comparable (see Witting et al., 1999): therefore year-to-year relative abundances could be estimated at that site. However, differences between sites are not easily compared because the catch efficiency of the two types of passive nets is not known and there is no independent estimate of absolute abundance at either site.

Age, growth, and birthdate determination

Larvae were randomly subsampled from individual weekly net sets at both locations in proportion to their contribution to the total nightly catch. All larvae in catches up to 20 fish were used. In catches of >20 fish, subsample sizes were proportional to catch but generally no more than 50 fish were aged per week from any one site. Experienced otolith readers at the Beaufort Laboratory determined the ages of 1435 larvae from North Carolina and 444 from New Jersey for our study. Larvae were measured to the nearest 0.1 mm standard length (SL) with an ocular micrometer. Estimated age was the number of sagittal otolith growth increments (Maillet and Checkley, 1990) plus an empirically derived value for the number of days (five) from spawning to first increment formation (Warlen, 1992). Additionally, late-larval to early-juvenile Atlantic menhaden reared in the laboratory through the winter at ambient water temperatures, formed daily otolith growth increments even when temperatures declined to 3°C (Ahrenholz et al., 2000). We assumed that the age at initial increment deposition in larval otoliths did not vary and that otolith increment deposition rate was constant within and between sampling seasons and the two sampling sites.

To reduce the chance of underestimating ages of larvae, we conducted a detailed examination of the otolith microstructure of larvae collected in the 1990–91 season. Otoliths from fish with our assigned January–February hatching dates were re-examined and their growth increments measured on an image analysis system. One reader made all counts and measurements in close consultation with two other experienced otolith readers. In contrast to the North Carolina larvae, New Jersey larval otoliths had areas in the middle portion of the counting path with narrower increments. However, New Jersey larvae did not have checks on their otoliths, which indicated that otolith growth did not stop. The otolith radius, standard length, and age relations suggested that New Jersey fish grew more slowly than North Carolina fish but did not indicate a systematic underestimation of the age of New Jersey fish due to narrow increments.

Average growth of larvae was described by the Laird version (Laird et al., 1965) of the Gompertz growth equation (Zweifel and Lasker, 1976). The model was fitted to

data for SL and estimated age at time of capture. To stabilize the variance of length over the observed age interval, length data were log-transformed and model parameters were estimated from the log-transformed version of the growth equation (Warlen, 1992). Because the conventional 3-parameter fit produced two cases where the estimates of the model intercept ($L_{(0)}$) were biologically unreasonable, all data sets were rerun by using a 2-parameter (i.e. $A_{(0)}$ and α) fitting procedure and by setting the intercept (third parameter) at 3.5 mm. This size at hatching was an intermediate value between the estimates of Powell and Phonlor (1986) for Atlantic menhaden hatching at 16° and 24°C. The overall average growth rate from hatching to a given age was the quotient of the predicted size at that age minus the size at hatching (3.5 mm) divided by that age. Differences in population growth curves between sampling locations in each year were tested by using a 2-parameter Hotelling's T^2 test of the model parameters (Bernard [1981] as modified by Hoenig and Hanumara[3]).

The birthdate (=spawning date) of each larva was back-calculated by subtracting its estimated age from the date of capture. Birthweek cohorts were defined as larvae spawned in a given calendar week. Density values and percentage age composition of each week's catch were used to estimate the estuarine recruitment of birthweek cohorts for each year and each location by using the methods of Warlen (1994). Birthdate distributions were used to estimate the percentage of larval recruits to the New Jersey estuary that could have originated in the SAB. The menhaden spawning season in North Carolina and New Jersey was estimated from the birthdate distributions of larvae that survived to enter the estuaries. The percentage distribution of spawning by week was based on the relative abundance of larvae collected throughout each recruitment year.

We assumed that larval Atlantic menhaden caught each week were newly recruited to the estuary and that they were in transit past the sampling sites to upper portions of the estuaries. This assumption is supported by the arguments in Warlen (1994), Churchill et al. (1999), and Forward et al. (1999) for the North Carolina sampling site and the patterns observed for other shelf-spawned estuarine dependent species such as summer flounder (*Paralichthys dentatus*) (Keefe and Able, 1993; Able and Kaiser, 1994) and other species for New Jersey (Witting et al., 1999).

Results

Timing and abundance of larval recruitment

The magnitude of larval Atlantic menhaden recruitment appeared to differ substantially between the two locations (Fig. 2). The sum of the weekly mean larval densities

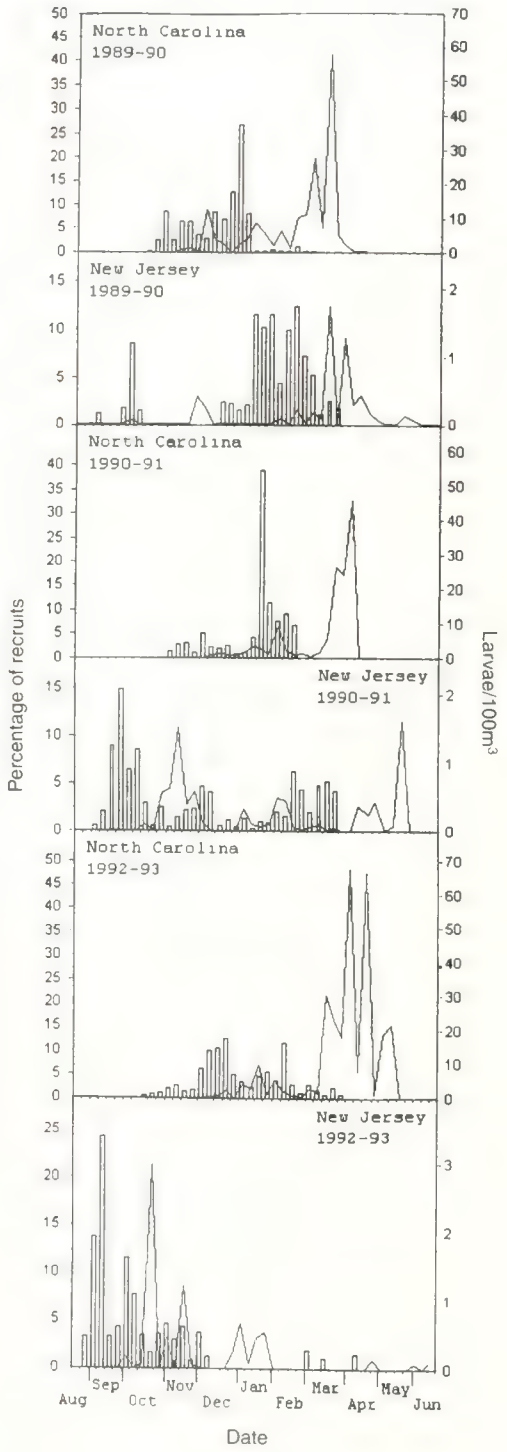

Figure 2

Weekly mean density (larvae/100 m^3) (line graph) and birthdate frequency distributions (bar graph) as calculated from relative abundances of larval Atlantic menhaden (*Brevoortia tyrannus*) in collections at Pivers Island, North Carolina, and Little Sheepshead Creek, New Jersey, during 1989–90, 1990–91, and 1992–93.

[3] Hoenig, N. A., and R. G. Hanumara. 1983. Statistical considerations in fitting seasonal growth models for fishes, 25 p. ICES council meeting 1983/D.

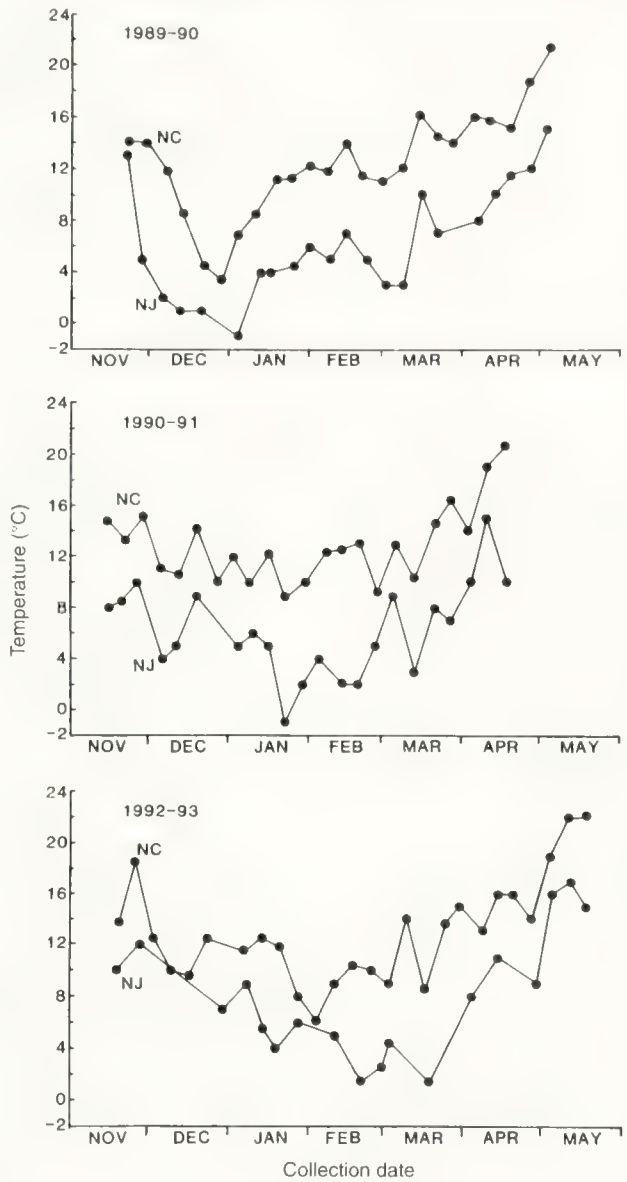

Figure 3

Surface water temperature at Pivers Island, North Carolina, and Little Sheepshead Creek, New Jersey, during collections in 1989–90, 1990–91, and 1992–93.

over all collections was a measure of the total abundance during a year. The total yearly densities (larvae/100 m^3) for North Carolina were 173 (1989–90), 128 (1990–91), and 286 (1992–93) and for New Jersey were 5.5 (1989–90), 8.4 (1990–91), and 7.3 (1992–93). Although there appeared to be generally large differences in overall abundance between the two areas, we could not determine how much of the 15–39× difference was due to the geographic location, the catch efficiency of the two types of gear, or to differences in sampling effort. Nightly mean densities were always low in New Jersey and, with one exception (20 October 1992), never exceeded 2.0 larvae/100 m^3, whereas in North Carolina nightly catches could exceed 40 larvae/100 m^3 every season (Fig. 2).

There were apparent differences in the timing of larval Atlantic menhaden entering estuaries in North Carolina and New Jersey (Fig. 2). Larval recruitment in New Jersey, which extended over a longer period (8–9 months) than that in North Carolina (5–6 months), began in October and ended in June (Fig. 2). Recruitment in New Jersey was discontinuous and was punctuated by periods of no catch, usually in late fall to early spring. The absences of

larval catches in some periods in New Jersey are associated with low water temperatures. There were no larvae caught in December–January of 1989–90 and 1990–91 and in February–March 1993 when water temperatures remained between 1.0 and 5.0°C (Fig. 3). In contrast, recruitment in North Carolina began in November and was continuous until ending in April or May (Fig. 2). Water temperature in North Carolina was warmer than in New Jersey and only twice dropped below 6°C (Fig. 3). In all three years in North Carolina, recruitment was characterized by a late season peak that occurred in March or April (Fig. 2). Predominant recruitment in New Jersey occurred either early (1992–93), late (1989–90) or with peaks early and late in the season (1990–91).

Larval age and size

Menhaden larvae entered both estuaries after development in the ocean. Most larvae were >1 month old and ≥ 17 mm long and there were no recently hatched specimens. However, the age and size of larvae entering the two estuaries differed within and between sites. The weekly mean age of Atlantic menhaden larvae collected in North Carolina increased linearly from early in the season to about the end of March in each year (Fig. 4). The weekly mean age over this period increased by a factor of 2–3×. In two years (1990, 1993) the mean age declined after March to levels approximating those early in the recruitment season. Larvae collected in the North Carolina estuary during peak recruitment were also the older (and larger) larvae. In New Jersey, although there was a general increase in larval age between October and December, there was no late season decline in mean age as we observed for North Carolina larvae. Larvae collected in New Jersey were generally younger than those collected in North Carolina for each of the three years (Fig. 5). The overall mean age of larvae collected in North Carolina for 1989–90, 1990–91, and 1992–93 were 60.7, 58.6, and 69.3 d as compared to 54.3, 52.7, and 50.9 d for New Jersey, respectively. The size of larvae showed seasonal trends similar to those for larval ages in each of the years, i.e. larval length increased and then decreased through time in North Carolina, whereas in New Jersey it increased but did not decline (Fig. 6). Larvae recruited in North Carolina were generally similar in size but were on average larger (24.9, 25.4, and 25.8 mm) than larvae recruited in New Jersey (22.2, 21.3, and 22.1 mm) in all three years (Figs. 6 and 7).

Growth of larvae

Larvae collected in North Carolina were generally older and larger and grew faster than larvae in New Jersey (Fig. 8). Population growth curves were significantly different between sampling locations in all years (Table 1). The predicted overall average growth rate from hatching to 65 d for larvae recruited in North Carolina was similar among years (0.35 mm/d for 1989–90, 0.36 mm/d for 1990–91, and 0.35 mm/d for 1992–93). Corresponding rates for larvae recruited to New Jersey were 0.30 mm/d for 1989–90, 0.31mm/d for 1990–91, and 0.32 mm/d for 1992–93.

Larval birthdates

Back-calculated spawning dates varied between years in both locations but were most variable in New Jersey (Fig. 2). In New Jersey in the 1989–90 season there were two distinct groups of larvae. About 13% of the larvae were spawned early (September–October), then none to the middle of December, and the remaining larvae (87%) were spawned thereafter to the end of March. Larvae captured in North Carolina were spawned from the week ending 21 October 1989 continuously through the week ending 3 March 1990 and overlapped the later spawning dates for New Jersey larvae. Larvae spawned in March recruited to New Jersey but virtually none recruited to North Carolina.

In the 1990–91 season, spawning dates of larvae collected in New Jersey (7 months) totally overlapped those collected in North Carolina (4 months) (Fig. 2). About 45% of the New Jersey larvae were spawned early (through week ending 27 October 1990) and the balance was distributed over the last five months with a mode in the week ending 23 February 1991. As in 1989–90, March-spawned larvae recruited to New Jersey but not to North Carolina. The highest frequency of spawning dates of larvae caught in North Carolina occurred from mid-January to the end of the season and peaked during the week ending 26 January 1991.

The spawning date distributions in 1992–93 were different from those in the previous two sampling seasons. About 77% of the New Jersey larvae were spawned by the end of October. An additional 18% of the total larvae entering the estuary were spawned in November to mid-December and only about 5% of the total were spawned in March–April. Larvae recruited to North Carolina had been spawned from October to April but there was no distinct mode as observed in the other two years. Late season spawning (March–April) contributed larvae to both New Jersey (≈5% of total) and North Carolina (≈13% of total). In both earlier years there were no April-spawned larvae and March-spawned larvae were only found in New Jersey.

Discussion

Atlantic menhaden larvae recruited to the New Jersey estuary probably originate from two sources: locally (MAB) and from the SAB. Evidence of local spawning is seen in the larvae recruited to the New Jersey estuary from October through early December (Fig. 2). These larvae probably originated from local (i.e. New Jersey) spawning as adults begin their southward migration out of the MAB area in about November of each year (Higham and Nicholson, 1964). Schools of spawning-size adults (200 mm+) are captured in the commercial fishery in the fall and early winter as they move south along the coast from Maryland to North Carolina (Smith[4]). Spawning in the SAB produces larvae, some of which are transported northward and contribute recruits to New Jersey later in

[4] Smith, J. W. 1996. Personal commun. Center for Coastal Fisheries and Habitat Research, National Ocean Service, NOAA, 101 Pivers Island Rd., Beaufort, NC.

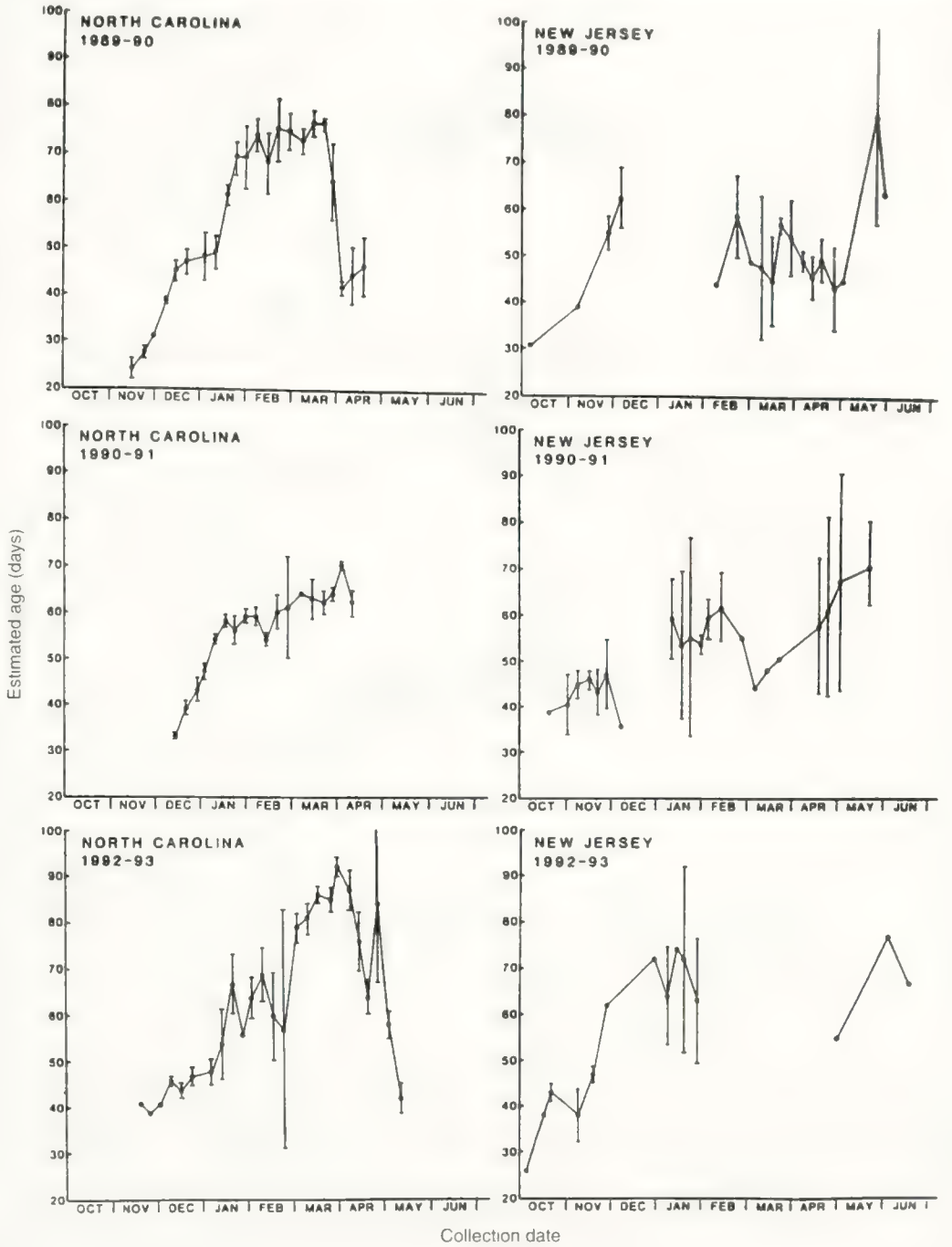

Figure 4

Mean of estimated age (days) with 95% confidence limits of larval Atlantic menhaden (*Brevoortia tyrannus*) collected weekly at Pivers Island, North Carolina, and Little Sheepshead Creek, New Jersey, during their estuarine recruitment in 1989–90, 1990–91, and 1992–93.

the recruitment season. Some larvae originating in the southernmost portion of the MAB in fall may even contribute some recruits to the SAB as three-dimensional circulation models have predicted (Quinlan et al., 1999; Rice et al., 1999; Stegmann et al., 1999). However, any adults that might remain in the MAB after November would experience ocean temperatures on the continental shelf that are not only too cold to allow menhaden spawning but that also might prevent eggs from hatching or larvae from developing. Even if we accept the minimum temperature of 13°C

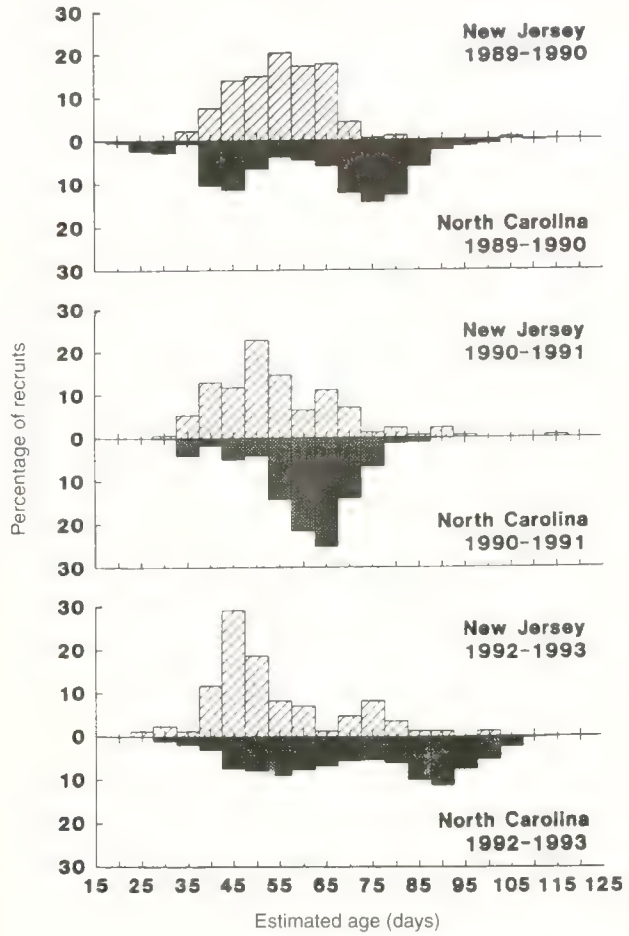

Figure 5

Percentage distribution of estimated age (5-d intervals) for larval Atlantic menhaden (*Brevoortia tyrannus*) recruited to Pivers Island, North Carolina, and Little Sheepshead Creek, New Jersey, in 1989–90, 1990–91, and 1992–93.

for Atlantic menhaden spawning suggested by Stegmann et al. (1999), there were no water temperatures above 12°C in the MAB in December through March (Fig. 9) during the three years of our study.

Two differing hypotheses could explain the occurrence of menhaden larvae recruiting to the New Jersey estuary in winter and spring. One is that larvae spawned in the MAB in October or November remain in the MAB until they move into estuaries in the spring. This hypothesis would require a retention mechanism to keep larvae on the continental shelf over the winter in water <10°C. No such mechanism is likely as field and modeling studies indicate persistent southwestward transport (Pietrafesa et al., 1994; Churchill and Berger, 1998; Werner et al., 1999). If larvae overwintered on the continental shelf, they would be about 150–210 d old when they recruited to the estuary 5–7 months after spawning. No Atlantic menhaden this old were found in any of the samples, or from any other studies (Warlen, 1994; Rice et al., 1999), and underaging of larval otoliths in our study did not appear to be a problem.

An alternative but more feasible hypothesis for the observed winter-spawned larvae collected in New Jersey from December to the end of the recruitment season (May–June) is that they were spawned in the SAB and were transported northward to the MAB. We used the density-weighted, back-calculated spawning date distributions of larvae collected in New Jersey that were spawned from November to April as the best estimator of the percentage of the total recruits that were spawned in the SAB. If we use the portion of larvae spawned December or later as the most conservative estimator, then the contribution of larvae from the SAB, of all New Jersey recruits, was 87% in 1989–90, 47% in 1990–91, and 10% in 1992–93. If larvae spawned November or later are considered to be from the SAB where there was spawning, then the estimate (87%) is the same for 1989–90 but increases to 55% in 1990–91 and to 23% in 1992–93.

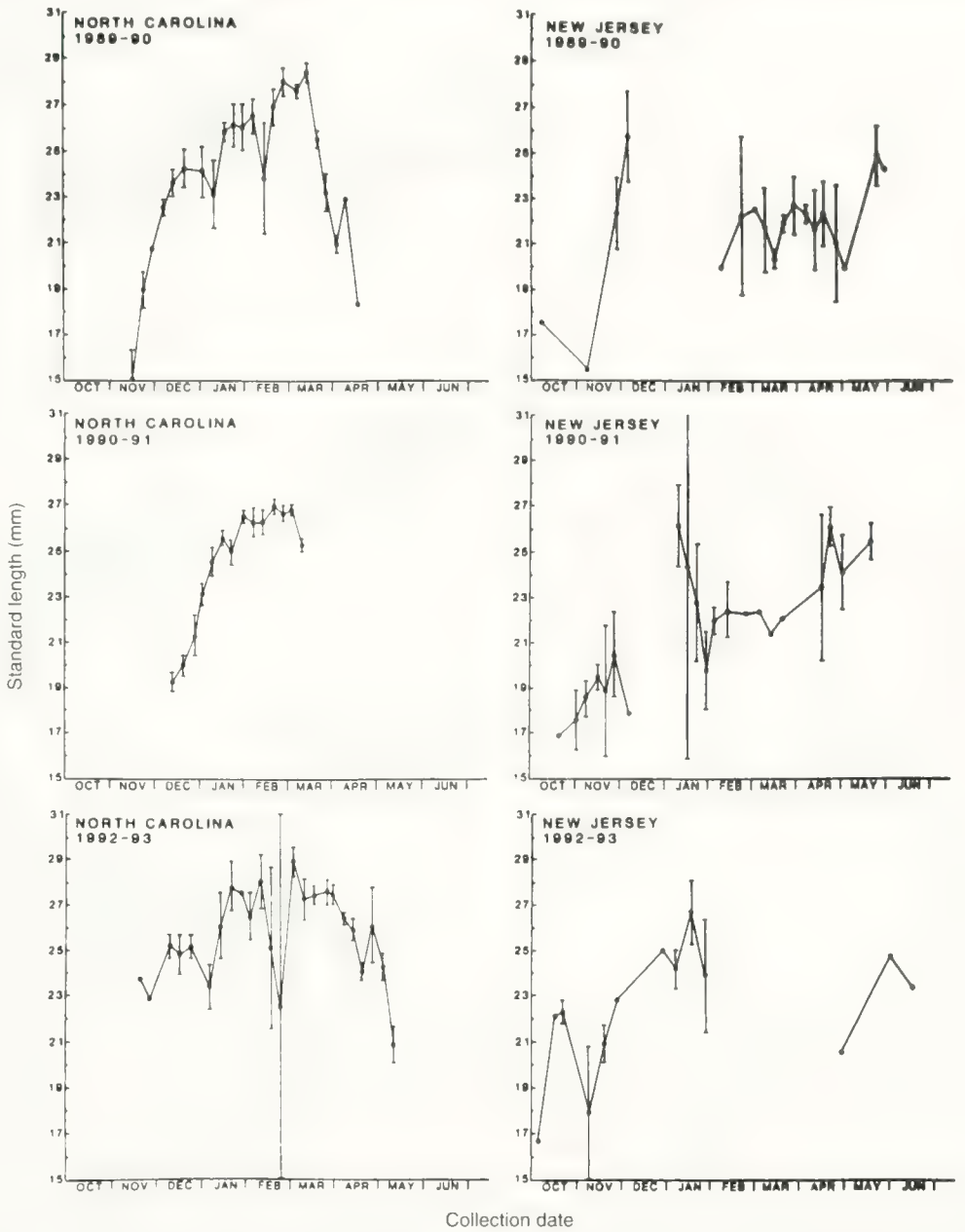

Figure 6

Mean standard length (mm) with 95% confidence limits of larval Atlantic menhaden (*Brevoortia tyrannus*) collected weekly at Pivers Island, North Carolina, and Little Sheepshead Creek, New Jersey, during their estuarine recruitment in 1989–90, 1990–91, and 1992–93.

Although the estimated percentage of larvae contributed to the New Jersey estuary from the SAB varied between 10% and 87%, the actual numbers of contributed larvae were relatively low, over an order of magnitude less than that observed for North Carolina, because of the overall low number of larvae recruited there. However, the total contribution of SAB larvae to New Jersey recruitment over the entire season may actually be greater than estimated from the birthdate distributions. The contribution of larvae spawned in the MAB to recruitment in New Jersey is based on the presence of early season larvae, but for these fish to contribute to the population the next spring, they must survive the winter in the estuary. If the winter water temperature in New Jersey estuaries drops below the lethal limit for Atlantic menhaden larvae (<5.0°C; Lewis, 1965), there will be decreased survival for the fall

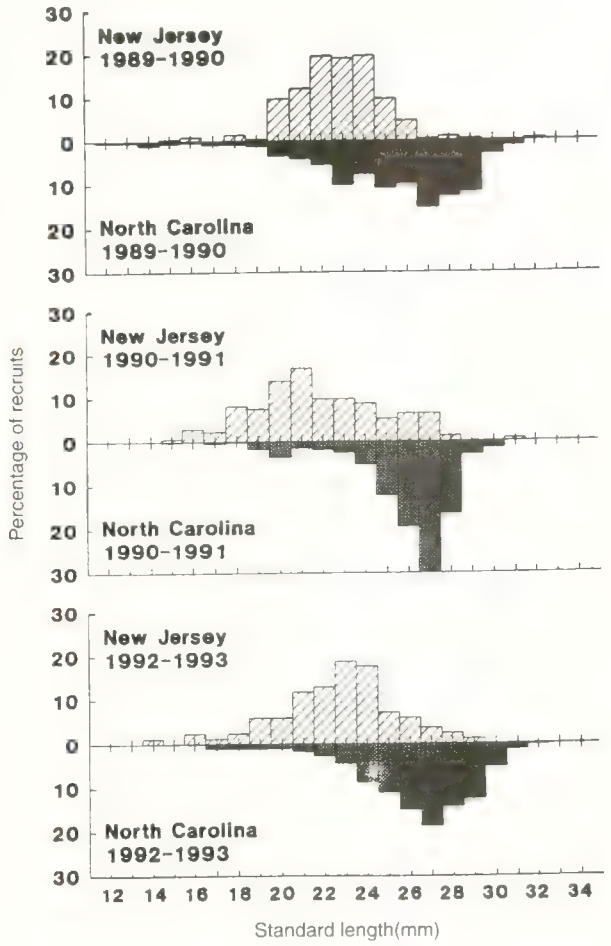

Figure 7

Percentage distribution of standard length (1-mm length intervals) for larval Atlantic menhaden (*Brevoortia tyrannus*) collected during their recruitment at Pivers Island, North Carolina, and Little Sheepshead Creek, New Jersey, in 1989–90, 1990–91, and 1992–93.

recruited larvae. Temperatures this low are often found during winter in New Jersey estuaries (Able et al., 1992) and result in mortality of several other estuarine species (Szedlmayer et al., 1992; Keefe and Able, 1993; Hales and Able, 2001). We did not catch Atlantic menhaden larvae in the New Jersey estuary at any time when the surface water temperature was <5°C. Temperatures <3°C deterred larval Atlantic menhaden entry into estuaries, inhibited movements into tributaries, and caused mass mortalities in Indian River, Delaware (Reintjes and Pacheco, 1966). Alternatively, larvae recruiting in March or later have less chance of encountering lethal temperatures and experiencing cold-related mortality and hence their proportion of the total year's recruitment may increase.

The precise mechanisms responsible for larval Atlantic menhaden transport from the SAB to the MAB are unknown. However, it seems likely that larvae may be transported northward by the Gulf Stream. Atlantic menhaden larvae that are spawned on the outer continental shelf of North Carolina (Checkley et al., 1988; Warlen, 1992; Govoni and Pietrafesa, 1994) may be entrained in meanders that impinge onto the shelf (Pietrafesa et al., 1985) and carried northward out of the SAB. Govoni and Spach (1999) estimated offshore fluxes of Atlantic menhaden larvae from the North Carolina shelf to the Gulf Stream during the winter. Modeling results supported these empirical findings and indicated that export from the North Carolina shelf is influenced by both wind and bathymetry (Hare et al., 1999). Once in the Gulf Stream, larvae can be transported rapidly (≈100 cm/s) to the northeast (Hare[5]).

Hare, J. A. 1999. Personal commun. Center for Coastal Fisheries and Habitat Research, National Ocean Service, NOAA, 101 Pivers Island Rd., Beaufort, NC.

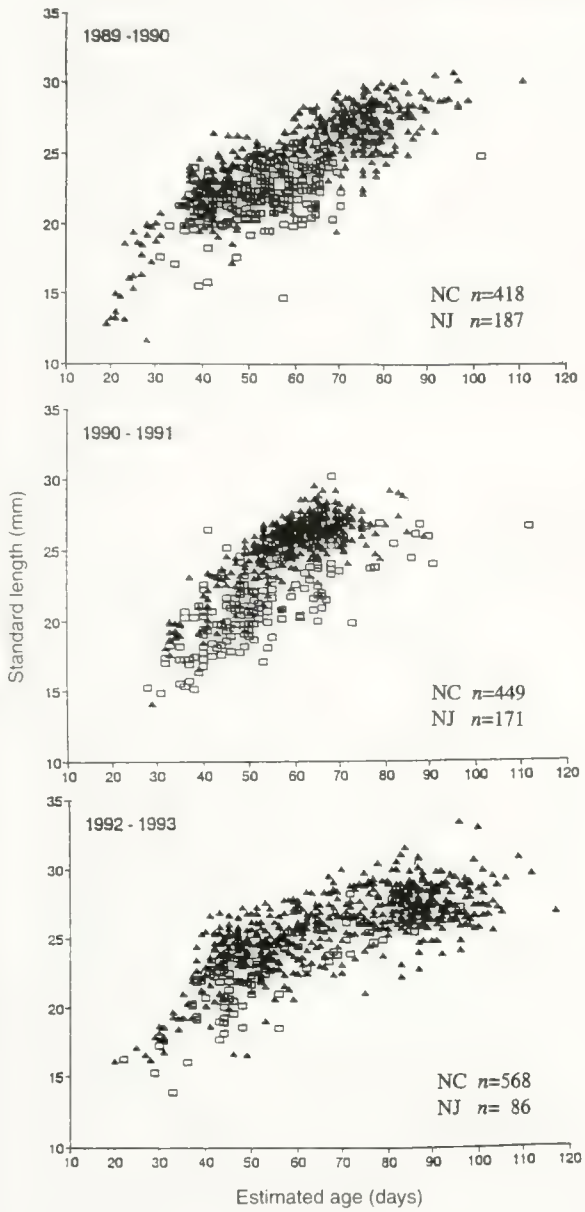

Figure 8

Summary plots of standard length (mm) on estimated age (days) for larval Atlantic menhaden (*Brevoortia tyrannus*) collected at Pivers Island, North Carolina, and Little Sheepshead Creek, New Jersey, in 1989–90, 1990–9, and 1992–93.

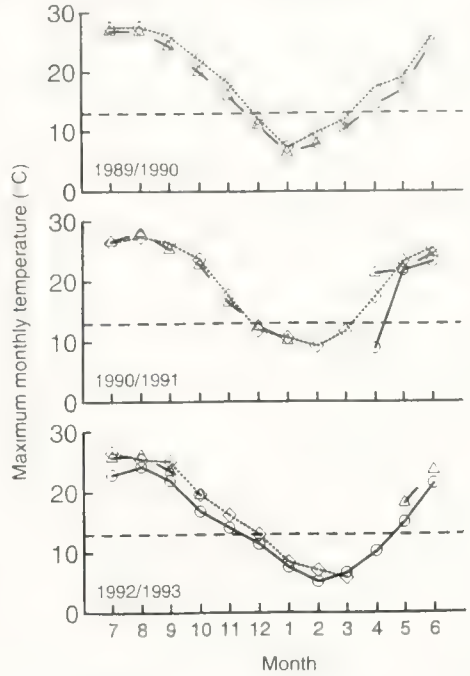

Figure 9

Maximum monthly sea surface temperatures recorded at three NOAA stations in the Middle Atlantic Bight that encompassed the time periods of our three sampling years. Minimum temperature that *Brevoortia tyrannus* eggs had been caught during MARMAP surveys (13°C; Stegmann et al., 1999) are indicated by a horizontal dashed line. In months with maximum temperatures below 13°C no spawning of *B. tyrannus* north of Cape Hatteras was expected. NOAA Data Buoy 44025 located ~45 km south of Long Island, New York at 40°15′1″N, 73°10′0″W. NOAA Data Buoy 44029 is located ~45 km southeast of Delaware Bay at 38°27′49″N, 74°42′7″W. NOAA C-MAN station CHLV2 is located ~20km east of Chesapeake Bay at 36°54′18″N, 75°42′48″W.

Warm core ring streamers and surface intrusions of warmer water could assist in transporting larvae from the Gulf Stream to the MAB continental slope (Hare and Cowen, 1991, 1996). Larvae must then cross the shelf-slope front and once larvae are in shelf waters they may be transported south and westward along the coast and toward shore by the predominant winds from the northeast which induce an Eckman drift westward toward shore. Biological mechanisms such as vertical migrations and directional swimming behavior, can modulate transport by placing larvae in water masses favorable to cross slope or cross shelf transport (Hare and Cowan, 1996). Cowen et al. (1993) and Hare and Cowen (1993) have described this general scenario for several species that may be transported to the MAB from the SAB.

Regardless of the type of transport mechanisms, it is clear that larvae of a number of other species are transported from the SAB to the MAB. The larvae of *Anguilla rostrata*, which originate in the Sargasso Sea (Schmidt,

Table 1

Estimates of Gompertz growth model parameters ($A_{(0)}$, α) with standard errors in parentheses for larval Atlantic menhaden collected in 1989–90, 1990–91, and 1992–93 in North Carolina and New Jersey and results of Hotelling's T^2 tests comparing growth models between sites for each year. In each model fit, $L_{(0)}$ was set at 3.5 mm standard length. * Significant at 0.01.

	Year		
Statistics	1989–90	1990–91	1992–93
Growth model[1]			
North Carolina			
$A_{(0)}$	0.113 (0.002)	0.101 (0.001)	0.113 (0.002)
α	0.054 (0.001)	0.048 (0.001)	0.055 (0.001)
New Jersey			
$A_{(0)}$	0.129 (0.008)	0.092 (0.003)	0.104 (0.005)
α	0.068 (0.005)	0.046 (0.002)	0.051 (0.003)
Hotelling's T^2			
Sample size			
n_1—NC	418	449	568
n_2—NJ	187	171	85
$F(0.01, f_1, f_2)$[2]	5.30	5.30	5.30
$F_{calculated}$	153.87*	127.81*	7.12*

[1] $L_{(0)}$ = length at hatching, $A_{(0)}$ = specific growth rate at hatching, α = exponential decline in $A_{(0)}$.
[2] 0.01 = level of testing, f_1 = np (=no. of parameters), $f_2 = n_1+n_2-np-1$.

1922; McCleave and Miller, 1994), occur in and near the Gulf Stream in the SAB and appear as glass eels in the New Jersey collections at approximately the same time as menhaden larvae (Witting et al., 1999). The same general track is presumed for *Conger oceanicus* which also spawn in the Sargasso Sea (Miller, 1995) and are also collected at the New Jersey study site, although they occur later (May–June) (Able and Fahay, 1998; Witting et al., 1999). Similarly, other species which presumably spawn in the SAB such as *Chaetodon* spp. (McBride and Able, 1998), *Mugil curema* (Collins and Stender, 1989), and *Lutjanus griseus* (Able and Fahay, 1998) also enter the New Jersey study site (Able et al., 1997; Witting et al., 1999). Larval spot, *Leiostomus xanthurus,* spawned south of Cape Hatteras may also be transported to estuaries in the MAB (Norcross and Bodolus, 1991).

In summary, although the SAB may be a very important spawning area for Atlantic menhaden, all larvae produced in the SAB are not retained there; some are transported to the MAB. We believe the birthdate distribution data suggest that Atlantic menhaden larvae spawned in the SAB are an important but variable source of recruits (10–87%) for the MAB based on the collections from New Jersey. The number of winter-spawned larvae ultimately recruited to New Jersey probably depends on the initial number of larvae transported northward from the SAB, the efficacy of the transport mechanisms, and the mortality of larvae during the process. Obviously, the estimates for this single New Jersey estuary may differ from other areas in the MAB. As a result of the above variables and recent insights from the SABRE program, it appears that larval Atlantic menhaden supply is very complex with frequent exchanges between the MAB and the SAB, as well as the contribution from local spawning. Ultimately, we need to know which spawning seasons and sites contribute most individuals to nursery habitats (Beck et al., 2001) and to the adult population.

The relative contribution of SAB menhaden larvae, and those of other species, to other estuaries in the MAB might clarify the importance of MAB estuaries and contribute to an improved understanding of recruitment mechanisms for shelf-spawned estuarine-dependent fishes in the MAB. Additional evidence for the contribution of SAB larvae to the MAB could come from analyses of the elemental composition of the primordium (nucleus) of larval otoliths from both New Jersey and North Carolina. The laser ablation inductively coupled plasma mass spectroscopy (ICPMS) technique (Campana et al., 1994; Thorrold et al., 2001) might be used to discriminate among larvae to determine if they have similar or different geographic origins. Similarities in elemental composition of New Jersey and North Carolina larvae with the same winter-spawned birthdate would be an important step toward validating the common geographic origin of the larvae recruited to New Jersey and perhaps elsewhere in the MAB.

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Origin of immature loggerhead sea turtles (*Caretta caretta*) at Hutchinson Island, Florida: evidence from mtDNA markers

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Abstract—Loggerhead sea turtles (*Caretta caretta*) are migratory, long-lived, and slow maturing. They are difficult to study because they are seen rarely and their habitats range over vast stretches of the ocean. Movements of immature turtles between pelagic and coastal developmental habitats are particularly difficult to investigate because of inadequate tagging technologies and the difficulty in capturing significant numbers of turtles at sea. However, genetic markers found in mitochondrial DNA (mtDNA) provide a basis for predicting the origin of juvenile turtles in developmental habitats. Mixed stock analysis was used to determine which nesting populations were contributing individuals to a foraging aggregation of immature loggerhead turtles (mean 63.3 cm straight carapace length [SCL]) captured in coastal waters off Hutchinson Island, Florida. The results indicated that at least three different western Atlantic loggerhead sea turtle subpopulations contribute to this group: south Florida (69%), Mexico (20%), and northeast Florida-North Carolina (10%). The conservation and management of these immature sea turtles is complicated by their multinational genetic demographics.

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North Atlantic loggerhead sea turtles have extended and complex developmental life histories (Musick and Limpus, 1997). After emerging from their nests, hatchling loggerhead sea turtles enter the surf and eventually move into the pelagic environment for several years before returning to inshore benthic coastal waters. The accepted hypothesis is that these hatchlings are passively transported to the eastern Atlantic by major current systems and these turtles would eventually return to coastal benthic habitats in the western Atlantic by the North Atlantic gyre when they attain 25–60 cm or an estimated 3–10 years old (Carr, 1986, 1987; Musick and Limpus, 1997).

The loggerhead sea turtle (*Caretta caretta*) is listed as threatened under the United States Endangered Species Act of 1973 and subsequent amendments. Although the loggerhead sea turtle nesting population in the southeastern United States is one of the largest in the world, other distinct nesting populations (as defined by genetic divergence) exist in the northwestern Atlantic Ocean. These known subpopulations are found in the Yucatan, northwest Florida, south Florida, and from north Florida to North Carolina. The east central coast of Florida supports the largest nesting subpopulation of loggerhead turtles and is a highly dynamic coastal area with multiple sea turtle species in various postpelagic developmental stages (Witzell, 1987). Sea turtles may hatch in one country, grow through adolescence in a second or more countries, feed and reproduce as adults in a third jurisdiction, and swim through a dozen more territorial waters enroute to and from these destinations (Bowen et al., 1995). Tagging studies, unfortunately, are only capable of providing glimpses of these complex changes in developmental habitats because of high tag loss rates and rare opportunities of recapturing tagged turtles thousands of kilometers away in the pelagic environment several years later (Chaloupka and Musick, 1997).

The likelihood that turtles from genetically distinct stocks share coastal and pelagic developmental habitats may raise doubts regarding the effectiveness of conservation strategies based on geographical or political boundaries (Carr and Stancyk, 1975; Bowen and Witzell, 1996). Consequently, sea turtle biolo-

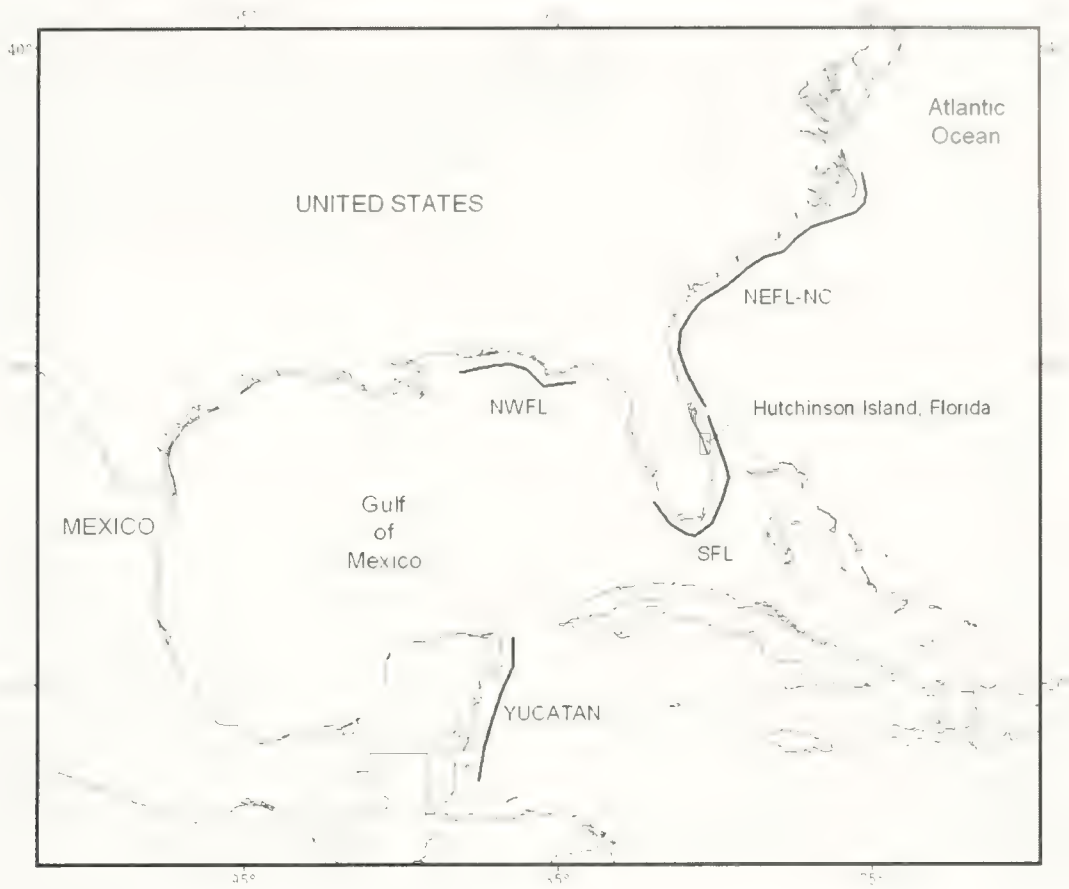

Figure 1

Locations for which are known loggerhead sea turtle nesting haplotypes and the location of the Hutchinson Island foraging population.

gists and marine resource managers are presented with complex challenges that reinforce the need for complete life history information. In particular, the origin of immature loggerhead sea turtles foraging in coastal nearshore waters needs to be determined for the development of effective regional conservation and management strategies. Recent research has demonstrated that most sea turtle nesting colonies are genetically distinct as indicated by mitochondrial (mt) DNA haplotype frequency shifts. This finding allows the possibility of using mtDNA data to identify rookery cohorts on feeding grounds (Bass et al., 1998; Broderick et al., 1994). By using an existing database (Encalada et al., 1998) and molecular techniques, tissue samples from juvenile marine turtles can be analyzed to estimate the origin of animals inhabiting developmental habitats. These data are collected and analyzed faster than results from tagging studies and may provide information on cryptic migratory behavior (Bowen et al., 1995; Bolten et al., 1998). Both pelagic and coastal benthic zones are believed to be essential developmental habitats for sea turtles, and molecular markers have recently been used to document shifts in the demographic composition between these habitats (Laurent et al., 1998). This article examines the mtDNA composition of juvenile loggerhead sea turtles using the coastal waters off Hutchinson Island, Florida, to determine whether the turtles are primarily from the adjacent nesting subpopulation or whether this foraging population is composed of individuals from multiple rookeries.

Materials and methods

Sea turtles are routinely captured in the canal that supplies cooling water at the St. Lucie Power Plant on Hutchinson Island, Florida (Fig. 1). The power plant intake operates year round—collecting sea turtles from 365 m offshore and providing an excellent opportunity to sample sea turtles in the nearshore developmental habitat (Bass and Witzell, 2000). Power plant biologists collect these turtles daily in an ongoing research and conservation program. Turtles are measured, flipper-tagged, and released in good condition promptly into the adjacent coastal waters.

A total of 109 juvenile loggerhead sea turtles were sampled at the St. Lucie power plant from January through May 1999 for our study. The minimum straight carapace length (SCL) was measured with calipers. Tissue samples were collected by using a 6-mm biopsy punch and placed in 15 mL of saturated salt preservation buffer developed

Table 1

Haplotype distribution among loggerhead sea turtle nesting groups compiled by Encalada et al. (1998). Haplotypes K and M were identified previously in the Madeira and Azores foraging assemblages (Bolten et al., 1998). Haplotype N was identified previously in a sample of stranded individuals from the Atlantic U.S. coast (Rankin-Baransky et al., 2001).

Haplotype	NWFL	SFL	NEFL-NC	Mexico	Greece	Brazil	St. Lucie, Florida
A	34	22	104				40
B	4	24	1	11	19		45
C	2	2	—	2			7
D			—			11	11
E	—	1	—		—	—	—
F			—			—	
G	2	1	—	—	—	—	—
H	—	—		1			
I	—	—	—	1	—		4
J	—	—	—	5	—		2
K	—		—		—		1
M	—	—	—			—	1
N		—		—			1

by Amos and Hoelzel (1991). Samples were transferred to the University of Florida for analysis. Standard phenol and chloroform DNA isolation protocols were conducted on the tissue samples (Hillis et al., 1996). A 380-bp fragment of the mitochondrial DNA control region was amplified using primers

TCR5 (5′-TTGTACATCTACTTAATTACCAC-3′), and

HDCM2 (5-GCAAGTAAAACTACCGTATGCCAGGTTA-3′)

designed for sea turtles (Encalada et al., 1996; Norman et al., 1994). Cycling parameters were as follows: 94°C 1 min, 25 cycles of (94°C/45s + 52°C/30s + 72°C/45s) and 3-min extension at 72°C.

Individuals were compared to known loggerhead sea turtle haplotypes and assigned a letter designation based on Encalada et al. (1998) and Bolten et al. (1998). To test for statistical differences among haplotype frequencies at rookeries and the foraging location, chi-square analyses were performed with the program CHIRXC (Zaykin and Pudovkin, 1993) and probabilities were generated with a Monte Carlo randomization procedure (Roff and Bentzen, 1989).

Maximum likelihood (ML) analysis for mixed stock identification (Grant et al., 1980) was used to estimate the contributions of nesting populations to the foraging habitat adjacent to the St. Lucie Power Plant on Hutchinson Island. This method estimates the most likely contributions of source populations based on the haplotype frequencies in the source populations and in the mixed population. The source populations and frequencies of associated haplotypes used in the analysis were those of Encalada et al. (1998). It should be noted that the addition of new nesting population data could change the results presented in our study. The addition of new nesting data will always be a problem when conducting these types of analyses but should not preclude the use of this technique to determine potential contributors to a foraging population. The maximum likelihood program GIRLSEM was used (Masuda et al., 1991). As a starting point in ML iterations with GIRLSEM, it was assumed that all source populations had an equal probability of contributing (i.e. population size, distance from the foraging location, etc. did not have an impact on the percentage of animals recruiting to a particular area). Standard errors and 95% confidence intervals of the point estimates were generated from 100 bootstraps of the stock and mixture data sets with GIRLSEM (Pella et al., 1998).

Results

Mitochondrial DNA analysis

Of the 109 tissue samples collected, 106 produced readable sequences (Table 1). Eighty five of the samples consisted of the most common haplotypes A and B. Haplotype C, another haplotype found in multiple rookeries at low frequency, was found in seven individuals. One individual was characterized by haplotype G, known only in the northwest Florida (NWFL) and south Florida (SFL) source populations. Two haplotypes "endemic" to Mexico (Yucatan), I and J, were found in six of the individuals sampled. The remaining seven individuals possessed haplotypes (K, M, and N) observed previously, but only from surveys of foraging or stranded individuals.

The haplotype frequencies of the foraging juveniles were significantly different from all nesting loggerhead sea turtle populations except for the SFL nesting population (χ^2=9.51, P=0.40). Although the haplotype frequencies were similar to that of the SFL nesting population, the presence of haplotypes not associated with the SFL popu-

Table 2

Maximum likelihood estimates of contribution by source populations to immature loggerhead sea turtles from the St. Lucie Power Plant (n=99). Estimates were generated by using UCON software (Masuda et al., 1991) Standard errors and 95% confidence intervals were generated from 100 bootstraps of both the stock and mixture using GIRLSEM. NWFL = northwest Florida; SFL = south Florida; and NEFL-NC = northeast Florida to North Carolina.

Source population	Contribution	Standard error	95% Confidence interval
NWFL	0.0912	0.1896	0.0479–0.1345
SFL	0.6681	0.3072	0.5979–0.7383
NEFL-NC	0.0366	0.1363	0.0055–0.0677
Yucatan	0.2040	0.1125	0.1783–0.2297
Brazil	0.0000	0.0000	-
Greece	0.0000	0.1555	0.0000–0.0355

Table 3

Maximum likelihood estimates of contribution by source populations to immature loggerhead turtles from the St. Lucie power plant (n=99). Estimates were generated by using UCON software (Masuda et al., 1991). Standard errors and 95% confidence intervals were generated from 100 bootstraps of both the stock and mixture by using GIRLSEM. The source populations NWFL, Brazil and Greece, were removed from the analysis. SFL = south Flordia; and NEFL-NC = northeast Florida to North Carolina.

Source population	Contribution	Standard error	95% Confidence interval
SFL	0.6965	0.2211	0.6527–0.7403
NEFL-NC	0.0984	0.1151	0.0756–0.1212
Yucatan	0.2050	0.1296	0.1793–0.2307

lation indicates that this nesting population is not the sole contributor to this foraging population.

Maximum likelihood analysis

The initial maximum likelihood analysis yielded estimates of contribution that were associated with high standard errors (Table 2). The estimate for NWFL had an extremely high standard error. This high standard error is an indication of sampling error associated with the source population (Epifanio et al., 1995). Because of the large standard errors, an attempt was made to reduce the complexity of solutions that were involved in the maximum likelihood algorithm's search. Removing a potential source population decreases the potential number of "answers," consequently reducing the standard errors about the mean estimates.

The maximum likelihood analysis was repeated, removing the smallest and most distant source populations (NWFL, Brazil, and Greece) as potential contributors (Table 3). In addition to the statistical assumption that the large variation associated with several estimates is partially due to sampling error, we also made some biological assumptions. By removing the source populations we assumed that they were not contributing to this foraging area at levels sufficient to detect in this ML analysis. The nesting effort in NWFL may include 100–200 turtles annually (Meylan et al., 1995), as compared to tens of thousands of turtles that nest in southern Florida. Hence, the Florida panhandle is an important nesting area, but is probably too small to detect with precision in ML analyses. The removal of Greece as a potential source population was based on the results of the first analysis that indicated that this source population did not contribute at detectable levels (Table 1). Brazil was also removed from the analysis because there were no indications (either from the observed haplotypes or from the initial ML analysis) that this population contributed individuals to the foraging population at Hutchinson Island.

The results from the final ML analysis provided the most realistic estimate of the genetic composition of this area (Table 3). This analysis indicated that the SFL subpopulations is a major contributor to the Hutchinson Island foraging population. In addition, the Yucatan nesting population also appears to contribute a significant percentage of individuals to this area. Although the small northeast Florida to North Carolina (NEFL-NC) rookery appears to contribute some individuals, the standard error is still large; therefore, the estimate is not precise. Individuals from the NEFL-NC nesting population are present, but an accurate estimate (finer than 7–12%) is not possible at this time.

The results of the analysis of the St. Lucie foraging population are provisional and there are several limitations to the maximum likelihood analysis. A major assumption of this type of analysis is that all potential source populations

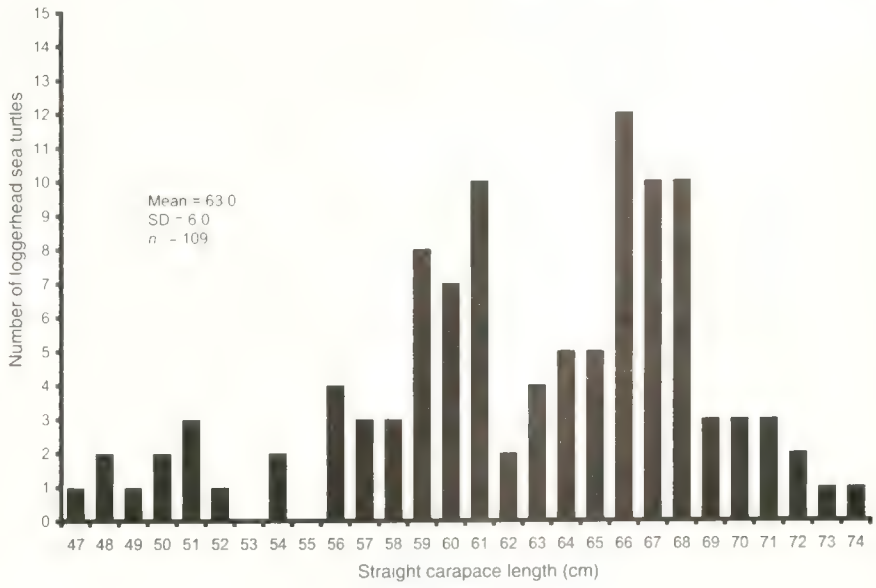

Figure 2

Length-frequency distribution for immature loggerhead sea turtles captured at the Hutchinson Island foraging ground (1999).

have been identified (Pella and Milner, 1987). Although the source population data set represents most of the major nesting colonies in the Atlantic, other nesting colonies exist that may contribute individuals to this foraging ground assemblage. For example, there are small nesting loggerhead populations on the Cape Verde Islands, Cuba, and on the coast of Colombia for which data are not accessible and we have been unable to estimate their possible contributions. If these nesting populations were included in the analysis there is a chance that the relative contributions of the source populations included in our study could be altered. A second major assumption is that the source populations were sampled sufficiently to uncover all haplotypes (Pella and Milner, 1987). In the case of the south Florida nesting assemblage, this assumption may not hold. As previously mentioned, south Florida supports the largest nesting assemblage in the Atlantic Ocean and it is possible that all haplotypes of the assemblage have not been determined. As with the inclusion of more potential source populations, there is the chance that changes in the frequency and distribution of haplotypes could alter the relative contributions reported in our study. We see these results as a sound starting point for the eventual analysis of foraging loggerhead sea turtles along the coast of the eastern United States.

The mean length of the 109 sampled turtles was 63.3 cm (SCL) with a standard deviation of 6.0 cm (Fig. 2). The mean lengths for all haplotype groups were very similar: for haplotypes A, B, C, and G (south Florida), mean length was 62.9 cm (±6.2); for haplotypes I and J (Yucatan), it was 63.8 cm (±8.0); and for haplotypes K, M, and N (other), it was 63.7 cm (±3.8).

Discussion

Although the estimates of percent contributions of the source populations generated here are provisional (i.e. more sampling of loggerhead nesting subpopulations may eventually uncover previously unrecorded haplotypes), they indicate that sea turtles foraging in the nearshore waters of Hutchinson Island originate from at least three rookeries in the Northwest Atlantic: SFL (69%), Yucatan (20%), and NEFL-NC (10%). Although the majority of animals appear to originate from Florida nesting beaches, the maximum likelihood analysis indicates that a substantial proportion of the foraging juveniles are coming from the southern nesting population in the Yucatan. In addition, the northern population, comprising animals nesting on beaches from northeast Florida to North Carolina, also contributes a smaller percentage of individuals.

Sears et al. (1995) reported on the demographic composition of juvenile loggerhead sea turtles off Charleston, South Carolina, and Norrgard and Graves (1995) analyzed juvenile loggerhead sea turtles from Chesapeake Bay, Virginia. Restriction fragment length polymorphism (RFLP) analysis of mtDNA was used to identify the genotype of individuals in both studies. The data sets were used in conjunction with a geographic survey limited to nesting locations in the North Atlantic Ocean and Mediterranean Sea by Bowen et al. (1993) to estimate the composition of these two areas. The estimates of contribution by nesting populations to these foraging areas (Table 4) appear to differ from the results presented in the present study, particularly the large contributions from the NEFL-NC haplotype. This may either reflect real differences in haplotype composition,

Table 4

Demographic compositions of coastal juvenile loggerhead sea turtles from U.S. coastal foraging habitats by using RFLP analysis. *n* = number of turtles in sample. SFL = south Florida; NEFL-NC = northeast Florida to North Carolina.

Location	SFL	NEFL-NC	*n*	Literature source
Chesapeake Bay	0.64	0.36	62	Norrgard and Graves (1995)
South Carolina	0.50	0.50	33	Sears et al. (1995)

inadequate sample sizes or sampling errors, or possibly changes between year classes. However, the differences are undoubtedly an artifact and are more likely due to the poor resolution and small sample sizes of the RFLP studies.

Comparisons of estimates generated by using different methods are problematic for several reasons. Recently, Encalada et al. (1998) published the results of a survey of nesting locations using sequences from the control region of the mtDNA. This region exhibits a sixfold increase in divergence rates when compared to estimates of divergence based on RFLP analysis. More variation was detected and consequently more haplotypes were identified than previously in Bowen et al. (1993). Encalada et al. (1998) also included several other nesting subpopulations in the Atlantic Ocean, in particular nesting subpopulations in northwest Florida and the Yucatan of Mexico.

The manner and routes of dispersal of posthatchling loggerhead sea turtles from the Yucatan and NWFL are undoubtedly complex and probably follow the same dispersal scenarios as proposed for the Kemp's ridley sea turtle (*Lepidochelys kempii*) by Collard and Ogren (1990). These loggerhead turtles either stay in the Gulf of Mexico or are transported into the Atlantic by the Florida Current. Once in the Atlantic, they either stay on the Continental shelf area or are entrained in major current systems and are transported to the eastern Atlantic Ocean for an undetermined amount of time before presumably returning to western Atlantic coastal benthic habitats. The SFL and NEFL-NC rookeries are all situated near the western boundary of the Gulf Stream where the hatchlings are quickly transported away from beaches. Juvenile loggerhead sea turtles leave their pelagic habitat over a range of sizes, and presumably ages, depending on feeding success. This estimate size range (SCL) was from 25 to 60 cm (Carr, 1986, 1987; Martin et al., 1989; Musick and Limpus, 1997). Hays and Marsh (1997) deduced from drift studies that the pelagic phase ended "at least for some loggerheads in the north Atlantic" when they were around 50 cm. These postpelagic turtles are thought to become coastal benthic crustacean foragers (Musick and Limpus, 1997) and to move up and down the U.S. East Coast seasonally.

Movements of juvenile loggerhead sea turtles tagged at the St. Lucie Power Plant indicate that a substantial portion of these turtles appear to reside in the immediate vicinity of Hutchinson Island (M. Bresette, unpubl. data). However, a few turtles have been documented from as far north as North Carolina and as far south as Florida Bay in southwest Florida. Most recaptured juvenile loggerhead sea turtles were from the north and may indicate that Hutchinson Island is near the southern boundary of the seasonal migration (Ernest et. al., 1989). Relatively few southern movements were recorded to Florida Bay. Over 47% of 3142 turtles under 85 cm captured at the St. Lucie Power Plant were captured from January through April 1976–2000 (Fig. 3). Captures then tapered off until December, consistent with seasonal north and south movements as suggested for immature turtles at nearby Cape Canaveral (Henwood, 1987). There has previously been no tagging evidence to indicate movements of these immature turtles outside the continental United States, yet these mtDNA data indicate a large contribution from Mexico.

The Hutchinson Island juvenile loggerhead sea turtles settle into this important coastal habitat at the same size, and presumably age, whatever their genetic origins are. This finding indicates that this particular coastal habitat may be critical for several western Atlantic populations of juvenile sea turtles, both loggerhead and green.

Management implications

The NEFL-NC population is of particular interest to some U.S. conservation biologists because of an apparent decline in nesting females prior to 1990 (Turtle Expert Working Group, 2000). The goal of protecting these turtles while in various developmental habitats is extremely complex, particularly when they intermingle with large numbers of sea turtles from a healthy (large) breeding population (SFL), as well as with small (NWFL) and foreign populations (Yucatan). Management measures affecting immature loggerhead sea turtles in the east-central Florida foraging habitats need to take into account the contributions from other source populations that may not be as robust as that of the south Florida population. Specific measures will depend largely on the demographic composition of stranded turtles with known sources of mortality. The genetic compositions of juvenile loggerhead sea turtles that are impacted by disease, boat collisions, anthropogenic debris, channel dredging, and recreational and commercial fisheries need to be determined before resource managers can take appropriate action. Unfortunately it is difficult to determine specific causes of mortality from stranded individuals, and researchers are unable to accurately determine the activities that affect specific nesting aggregations. The conservative approach would be to regulate all known sources of mortality to immature coastal loggerhead sea turtles until more data become available through aggressive genetic sampling and necropsies of stranded animals.

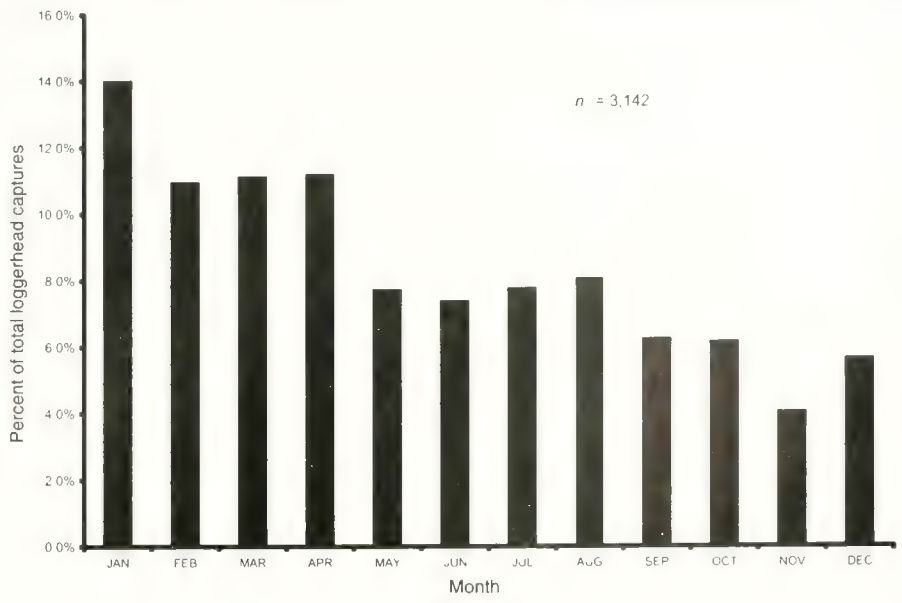

Figure 3

Monthly captures of loggerhead sea turtles less than 85 cm SCL at the St. Lucie Power Plant (1977–98).

The coastal foraging habitat near Hutchinson Island is also an important developmental habitat for endangered immature green sea turtles, *Chelonia mydas* (Bass and Witzell, 2000). This is a highly cosmopolitan species with contributions to the Florida foraging grounds from Costa Rica (53%), the United States and Mexico (42%), and Venezuela and Surinam (4%). It may be advisable for managers to designate specific areas, such as Hutchinson Island, as critical developmental habitats for immature sea turtles and to restrict public access.

The need for regional and internationally coordinated sea turtle research and management becomes obvious as genetic analysis reveals the complicated mixed stock of foraging turtle aggregations. International organizations, such as the International Union for the Conservation of Nature (IUCN) and the Intergovernmental Oceanographic Commission (IOCARIBE) need to become actively involved with the appropriate regional agencies of government to ensure the protection of sea turtle stocks in regional as well as international waters.

Acknowledgments

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Spawning of American shad (*Alosa sapidissima*) and striped bass (*Morone saxatilis*) in the Mattaponi and Pamunkey Rivers, Virginia*

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In the Atlantic coastal region, American shad (*Alosa sapidissima*) is highly prized for its flesh and roe. Spawning runs have been heavily fished and since the late 1800s, landings have shown steady declines to the extent that Maryland declared a fishing moratorium in 1980, and Virginia followed in 1994 for Chesapeake Bay and its tributaries (ASMFC, 1999). Shad restoration projects are underway to restock depleted spawning runs, especially in regions where stream impediments have been or are being removed. Coastal ocean intercept gill-net fisheries have remained in place despite criticism and speculation about their impact on populations, particularly those river systems stocks that are depleted. The Atlantic States Marine Fisheries Commission Shad Board (ASMFC, 1999) adopted a fishery management plan for American shad and river herring that included a five-year phase-out of the ocean fishery and that required states to develop an approved fishing or recovery plan for each stock under restoration. In Virginia, this requirement applies to the James and York rivers.

Although the roe fishery for American shad has historically been important, there is little information about the specific spawning locations of these broadcast spawners. American shad are anadromous fish native to the Atlantic coast of North America, with a range extending from southeastern Labrador to the St. Johns River, Florida. In Chesapeake Bay tributaries, American shad deposit semidemersal eggs in the freshwater portions of the estuaries in the spring, usually beginning in March and ending by early June with peaks in April (Klauda et al., 1991). American shad have historically ascended farther upriver than at present, within tributaries where obstructions to movements upstream now exist. Prior to dam building in the 1800s on the James River, large numbers of American shad traveled over 335 miles from Chesapeake Bay into the Jackson and Cowpasture rivers (Mansueti and Kolb, 1953).

The York River, a coastal plain tributary located in the Chesapeake Bay watershed, is formed by the confluence of the Pamunkey and Mattaponi Rivers at West Point (Fig. 1). The Pamunkey River has a larger watershed (3768 km^2) and average spring discharge rate (47.5 m^3/s) than the Mattaponi River (2274 km^2; 27.2 m^3/s, respectively). Watershed sizes are based on U.S. Geological Survey digital line graph data (DLG) at 1:100,000. On these unobstructed rivers, annual releases of hatchery-reared American shad approximate two to four million fry through efforts of the Virginia Game and Inland Fisheries (VGIF) and an estimated 2.5 to 3 million fry are released by the Pamunkey tribal government. In addition there are unknown contributions from the Mattaponi tribal government (Gunther[1]). Current monitoring of adult catches indicates that the York River supports the strongest runs of shad in Virginia (Olney and Hoenig[2]). American shad in the York River are used as the source stock for hatchery efforts in the James and Potomac rivers. Thus, the restoration efforts in Virginia are dependent on the productivity of the York River.

Within the freshwater tidal portions of the Mattaponi and Pamunkey rivers, numerous other species spawn, including striped bass (*Morone saxatilis*) (McGovern and Olney, 1988; Grant and Olney, 1991). The Chesapeake Bay stock has rebounded after severe declines in the 1970s and early 1980s as a result of successful management and several years of successful reproduction (Olney et al., 1991; Field, 1997). The extent of the spawning area for both American shad and striped bass is in part a function of salinity and temperature. Striped bass spawn from the limit of brackish water to freshwater in the rivers of Chesapeake Bay from early April through the end of May (Setzler-Hamilton et al., 1981), and American shad spawn in freshwater (Leim, 1924). McGovern and Olney (1996) noted that the lower limit of striped bass spawning followed the 1 ppt salinity contour, and Secor and Houde (1995) postulated that the freshwater-saltwater interface may act as a down-river barrier to striped bass egg and larval advection. Based on suitable temperature ranges (12–24°C for striped bass [Setzler-Hamilton et al., 1980; Rutherford and Houde, 1995] and 12–25°C for Ameri-

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[1] Gunther, T. 2000. Personal commun. Virginia Game and Inland Fisheries, Richmond, Virginia 23230.

[2] Olney, J. E., and J. M. Hoenig. 2000. Monitoring relative abundance of American shad in Virginia's Rivers. March 1998–1999. Final report to the U.S. Fish and Wildlife Service and Virginia Marine Resources Commission, 53 p. Contract number F-116-R-1. Virginia Institute of Marine Science, Gloucester Point, Virginia.

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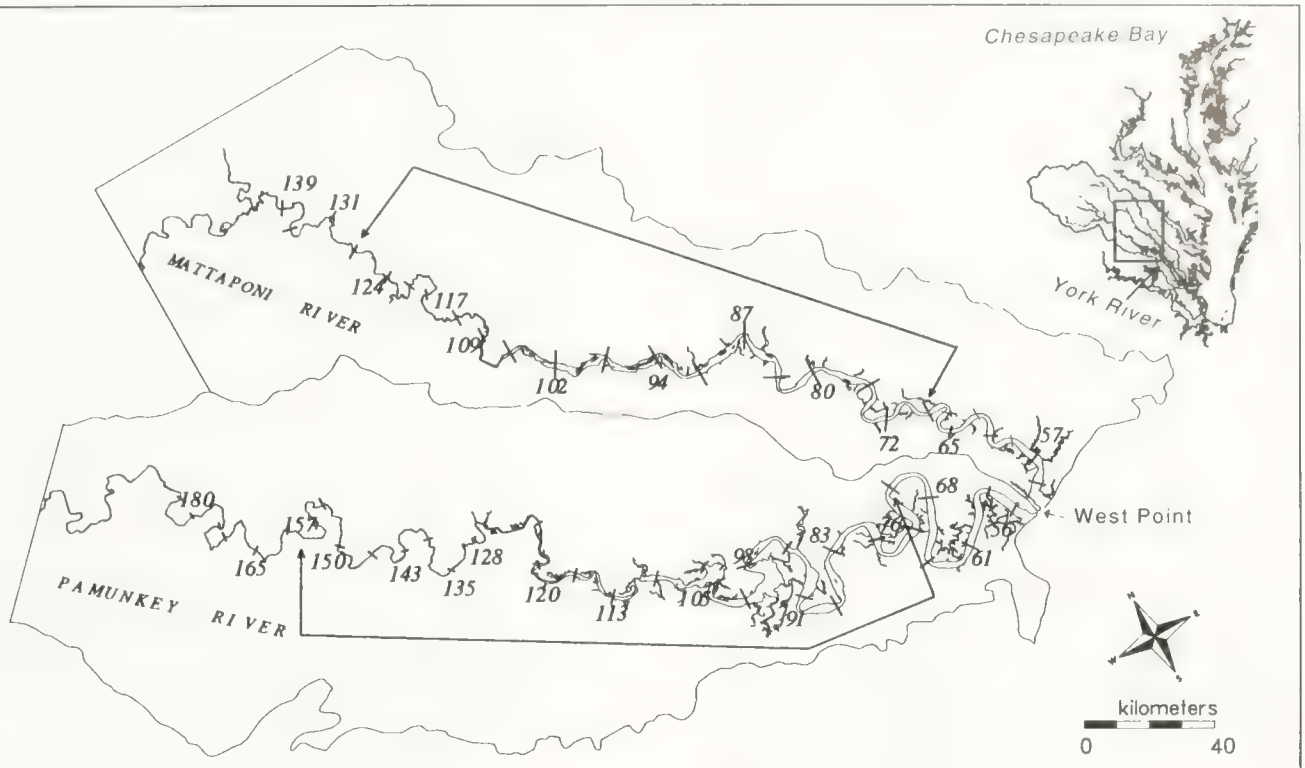

Figure 1

Extent of ichthyoplankton sampling by bongo net and pushnet in the Mattaponi and Pamunkey rivers (1997–99). Stations are denoted as the number of kilometers from the mouth of the York River.

can shad [Leach and Houde, 1999; Walburg and Nichols[3]] and salinity requirements for the early life stages of these species, the potential for spawning overlap spatially and temporally is high. Species interactions, including predation and competition by both adults and young, may play a role in the spawning and recruitment success of these species. Similar interactions have been postulated between American shad and other alosines in the Hudson River (Schmidt et al., 1988).

Our objectives were to describe the American shad spawning reaches in the Mattaponi and Pamunkey Rivers spatiotemporally, and to determine if striped bass also spawn within the identified spawning habitat of American shad. In year one, we completed an exploratory survey to map the distribution of the American shad spawning ground and the occurrence of striped bass within these reaches. In years two and three, sampling was modified to locate the upper limit of American shad and striped bass spawning within the two rivers.

[3] Walburg, C. H., and P R. Nichols. 1967. Biology and management of the American shad and the status of the fisheries, Atlantic coast of the United States, 1960. U.S. Fish and Wildlife Service, Special Scientific Report–Fish 550, 105 p. Fish and Wildlife Service, U.S. Dep. of Interior, Washington, DC 20005.

Materials and methods

Sampling protocol in 1997

Exploratory sampling in the Mattaponi and Pamunkey rivers for eggs and larvae of American shad and striped bass extended from March through April 1997. Sites were chosen on the basis of a prior survey of American shad eggs in the rivers (Massmann, 1952). Sampling protocol included weekly ichthyoplankton collections during daylight hours with stepped oblique tows of a bongo frame fitted with two 333-µm mesh nets (60-cm diameter). Catches from both nets were combined. The same ten stations were sampled weekly on each river within the tidal freshwater reaches. Stations are depicted as river kilometers (rkm) from the mouth of the York River, for example, M68 is a station on the Mattaponi River that is approximately 68 river kilometers from the mouth of the York River. The stations were located at approximately 3.2-rkm intervals within the range of 72 to 106 rkm (P72 to P106) on the Pamunkey River and 68 to 102 rkm (M68 to M102) on the Mattaponi River (Fig. 1).

Sampling protocol in 1998 and 1999

In 1998 and 1999, station locations were extended upriver to include more shallow stations owing to the low abun-

dance of American shad eggs in 1997. Bongo nets could not be used, and sampling included pushnet surveys in the upper reaches of the rivers (from 31 March through 20 May 1998 and from 11 April through 7 May 1999). The weekly sampling on each river consisted of pushnet tows at approximately one meter below the surface at each station. A pushnet frame fitted to the bow of a 14-foot boat (Olney and Boehlert, 1988) accommodated two plankton nets (333 μm, 60 cm). Catches from both nets were combined. In 1998, eight stations per river were systematically sampled bracketing M94 to M120 and P109 to P131. In 1999, two stations at M124 and M128 were added on the Mattaponi River; we added six upriver stations (P135–P154) and one downriver station (P104) on the Pamunkey River (each spaced at 3.2-rkm intervals, Fig. 1). Bongo and push nets were fitted with a flow meter for volumetric measurements and tow times were adjusted (three to seven minutes) to meet a lower limit of 50 m^3 of water filtered through both nets combined.

Laboratory procedures and data analysis

Ichthyoplankton samples were preserved in 10% phosphate-buffered formalin. Ichthyoplankton were sorted and larval fish and eggs were identified (Lippson and Moran, 1974; Jones et al.[4]), enumerated, and removed from the original, whole sample. Densities were reported as number per 100 m^3. Relative abundance in both rivers was calculated by average density of each life stage (egg, yolksac larva, and postyolksac) multiplied by total volume of spawning or nursery area sampled. Total volume of spawning or nursery area sampled was determined separately for each species by including locations within the sampling region where eggs (spawning reaches) or larvae (nursery reaches) were collected. River volumes were calculated by using bathymetric surveys and corresponding areal estimates from a digitized record of the mean high-water shoreline position as shown on the 7.5 minute topographic map series of the U.S. Geological Survey completed by Comprehensive Coastal Inventory, Virginia Institute of Marine Science (Bilkovic, 2000). For purposes of comparison, we used data on the abundance of American shad and striped bass juveniles in the Pamunkey and Mattaponi rivers. The data were taken from annual surveys of juvenile abundance conducted by the Virginia Institute of Marine Science (Austin et al., 2000; Olney and Hoenig[2]).

Results

Trends in density (numbers/100 m^3) of eggs for each river and species by date and station are depicted for 1997–99 in Figures 2 and 3. Average density (total eggs or larvae per total volume filtered) of each species per river is depicted in Figure 4. On the Mattaponi River (1997–99), American shad eggs were collected over a 44-km reach (M81–M124) and the highest densities occurred between M96 and M124. Striped bass spawning occurred over a 27-km reach and the highest densities in the sampled area occurred between M68 and M87, downstream of the primary spawning reaches of American shad (Figs. 2–4). On the Pamunkey River, American shad eggs were collected over a 53-km reach (P98–P150), and the highest densities were found between P104 and P131. Striped bass spawning occurred over a 60-km reach (P72–P131), and the highest densities were found between P72 and P87. There was some spatial overlap in spawning of these species, but the primary spawning reaches were separate. Temporal overlap in spawning of American shad and striped bass occurred throughout the sampled period in both rivers (Figs. 2–3).

On the Mattaponi River, American shad larvae (total length, 6.1–19.2 mm) were collected from M68 to M124, and the highest densities were observed between M94 and M102—a reach that is downstream of the spawning habitat. On the Pamunkey River, American shad larvae (total length, 6.6–12.2 mm) were collected between P76 and P128. Densities were highest at P102, 105, and 124. Larval striped bass were collected from M68 to M94 and from P72 to P109, and peak catches (>1/m^3) were collected from M68 to M80 and from P72 to P91. In both rivers, we observed overlap in American shad nursery grounds and striped bass spawning reaches. However, the highest densities of larval striped bass were downstream of the primary shad spawning and nursery areas (Fig. 4).

Average density of individual life stages of American shad was higher in the Mattaponi River than in the Pamunkey River; the opposite pattern was apparent for striped bass (Table 1). Estimates of the relative numbers of American shad and striped bass (average density × river volume) suggested that abundance of American shad eggs and larvae was higher on the Mattaponi River than on the Pamunkey River by a factor of 5.5 and 4.4, respectively. Relative abundance of striped bass eggs and larvae was higher on the Pamunkey River than on the Mattaponi River by a factor of 29 and 9.9, respectively (Table 2).

Discussion

Over the three years of surveys, eggs and larvae of American shad were rare compared to those of striped bass (Table 1). Despite our successive efforts to relocate sampling stations upstream of known striped bass spawning habitat (Grant and Olney, 1991; Olney et al., 1991), striped bass eggs and larvae were more abundant (~114 times and ~38 times, respectively) than those of American shad (Table 2). These differences could be attributed to the relative sizes and egg production of the spawning stocks because the number of mature American shad presently in the York River system is believed to be low in relation to historic run sizes (Nichols and Massmann, 1963; Olney

[4] Jones, P. W., F. D. Martin, and J. D. Hardy Jr. 1978. Development of fishes of the mid-Atlantic Bight. An atlas of egg, larval, and juvenile stages. Vol. 1, Acipenseridae through Ictaluridae. U.S. Fish and Wildlife Service report FSW/OBS-78/12. Fish and Wildlife Service, U.S. Dep. Commer., Washington DC 20005.

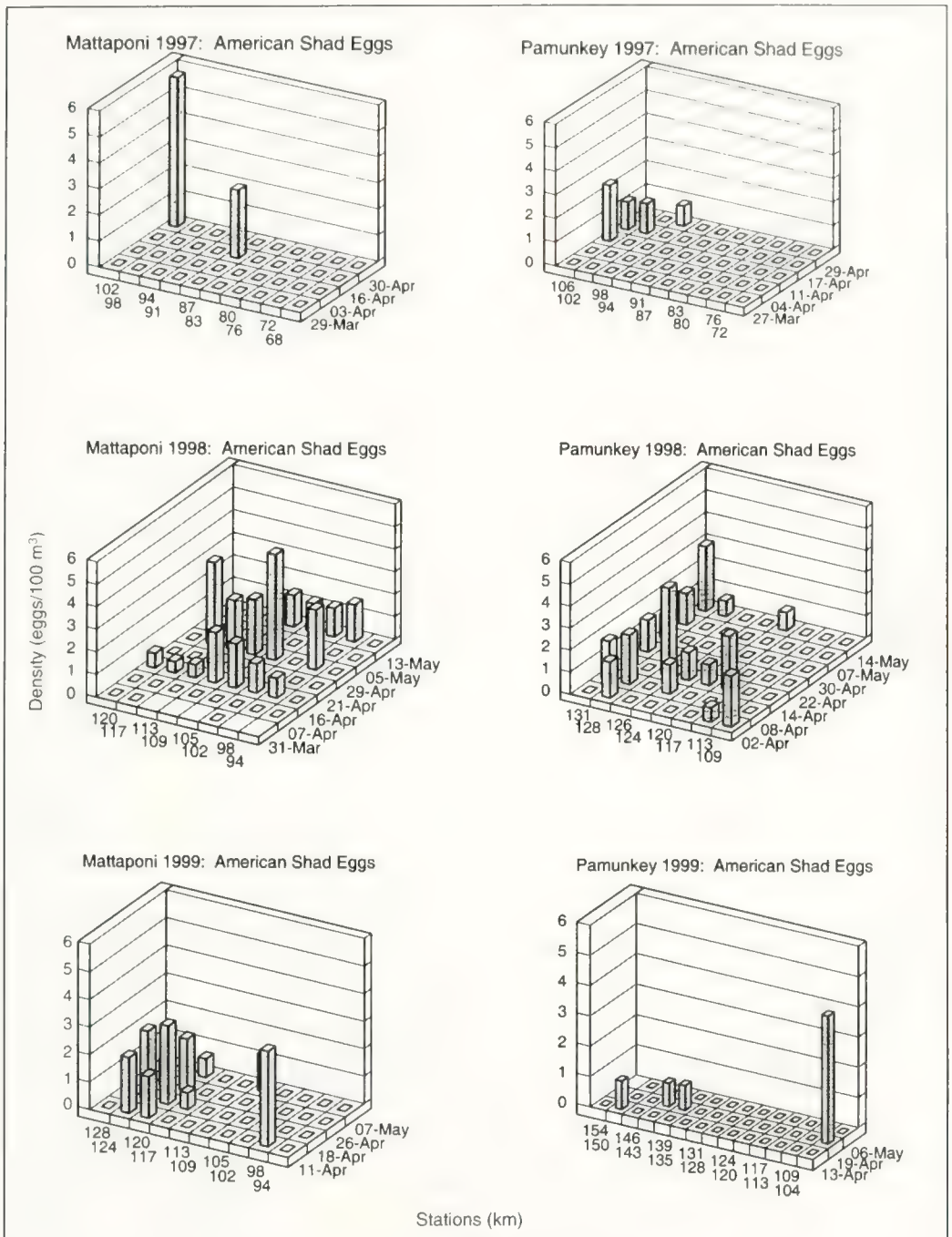

Figure 2

American shad egg density and distributions for 1997–99 bongo and pushnet collections. Stations are denoted as their distance (in kilometers) from the mouth of the York River.

and Hoenig[2]). In contrast, striped bass stocks are at record levels of abundance (Field, 1997) and support a large recreational and commercial fishery in the York River.

Despite the proximity and resemblance of the Pamunkey and Mattaponi Rivers, patterns of spawning and recruitment of American shad and striped bass are opposite for each tributary. We observed annual differences in abundance of eggs and larvae of these species that are concordant with indices of juvenile production. In our surveys, eggs and larvae of American shad were more abundant on the Mattaponi River and striped bass eggs and larvae were more abundant on the Pamunkey River (Tables 1 and 2). Similarly, mean recruitment (the mean index of juvenile abundance or JAI) of American shad

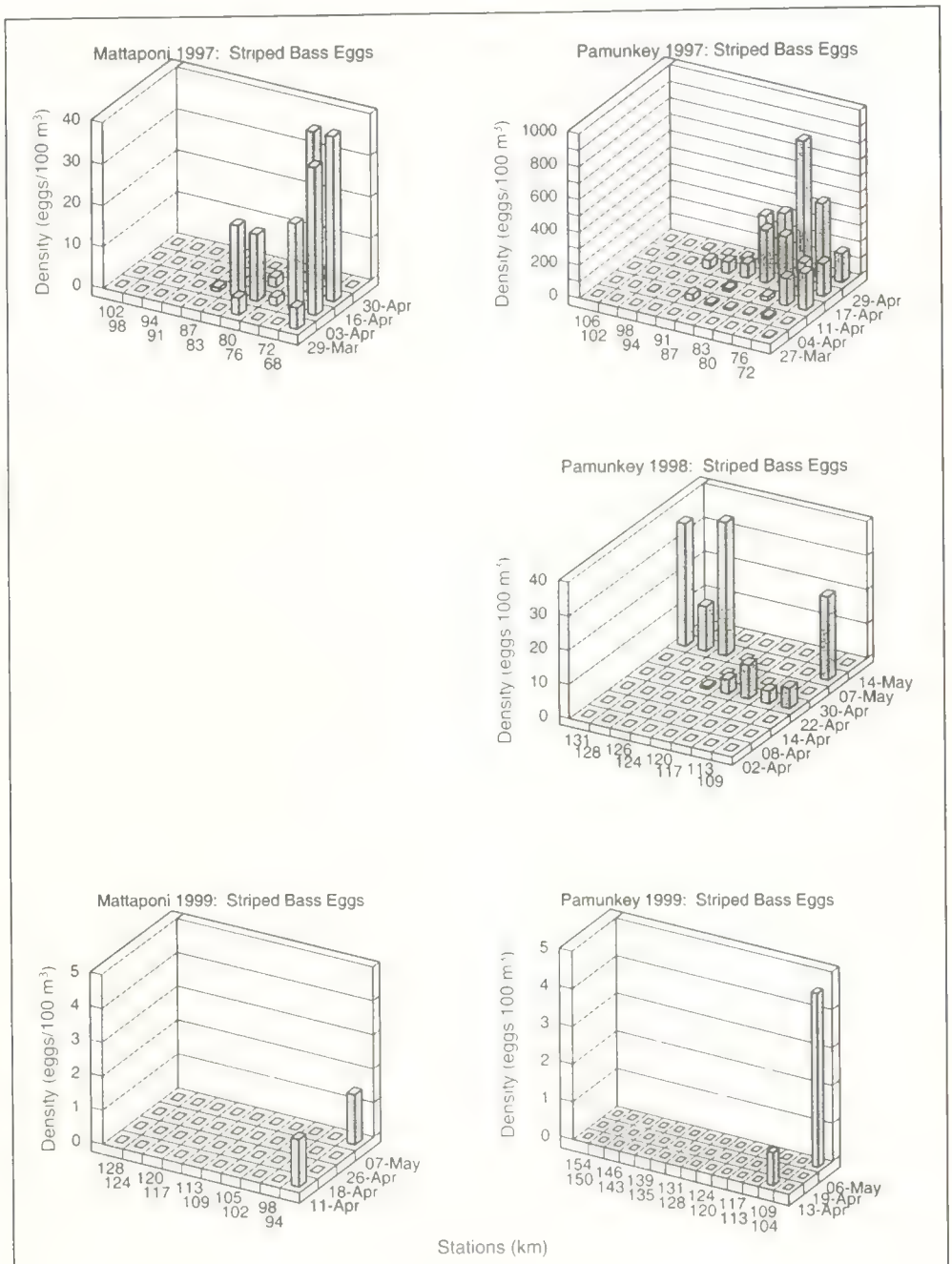

Figure 3

Striped bass egg density and distributions for 1997–99 bongo and pushnet collections. Stations are denoted as their distance (in kilometers) from the mouth of the York River. In 1998, no striped bass eggs were collected on the Mattaponi River.

was higher on the Mattaponi River (1997–99; Mattaponi JAI, 1648.5; Pamunkey JAI, 112.7), and mean recruitment of striped bass was higher on the Pamunkey River (1997–99; Mattaponi JAI, 1.6; Pamunkey JAI, 4.9). The approximate volume of the Pamunkey River, from the fall line to river mouth (1.9×10^8 m^3) is 1.2 times that of the Mattaponi River (1.6×10^8 m^3). Thus, equal populations of eggs or larvae that are homogeneously distributed on each tributary would be expected to be at the most 1.2 times as concentrated on the Mattaponi River. Because we observed differences in egg density that were much greater than double (~17 times in the case of striped bass) and in the unexpected direction (Pamunkey River egg densities > Mattaponi River egg densities), it is unlikely that

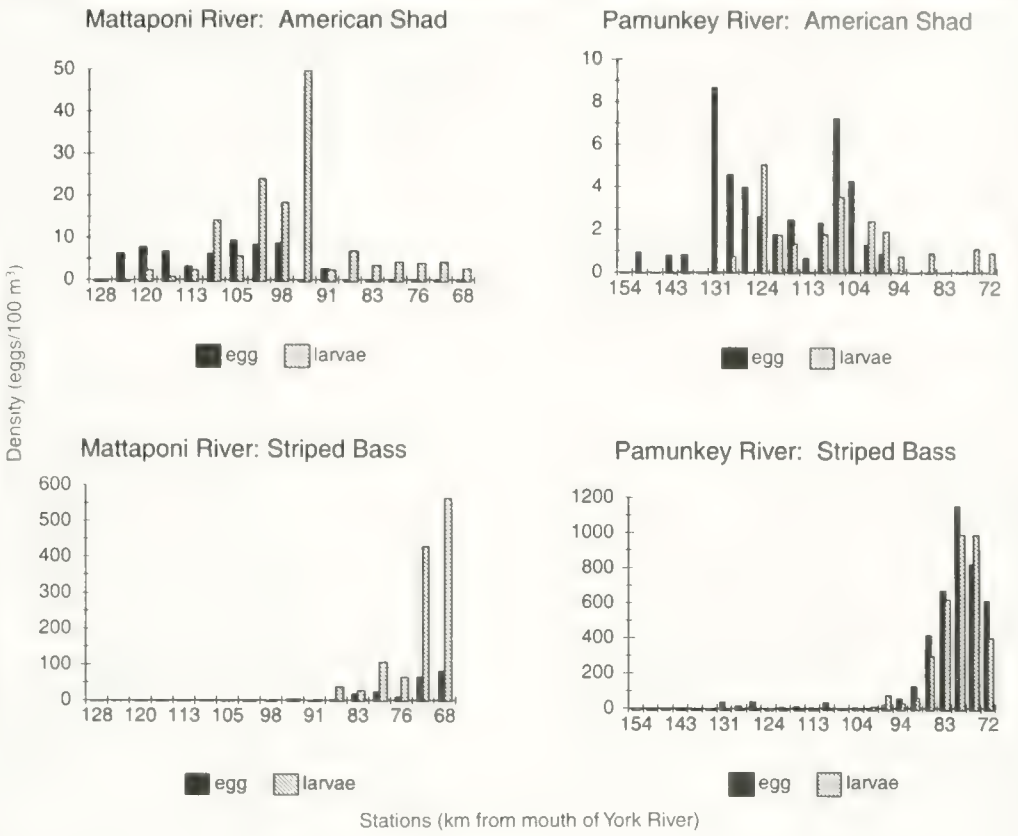

Figure 4

Total American shad and striped bass density (eggs and larvae) distinguished by river, species, and life stage for 1997–99 bongo and pushnet collections. Note differences in scaling on the y-axis.

Table 1

Average density (total numbers/total volume filtered) of eggs and larvae of American shad (*Alosa sapidissima*) and striped bass (*Morone saxatilis*) collected in the Mattaponi and Pamunkey rivers, Virginia (1997–99). Values are reported as numbers per 100 m^3.

			Larvae		
Species	River	Eggs	Yolksac	Postyolksac	Total larvae
American shad	Mattaponi	59.1	32.8	67.3	100.1
	Pamunkey	33.7	11.5	6.2	17.6
Striped bass	Mattaponi	205.3	392.1	792.4	1184.5
	Pamunkey	4016.5	2625.9	909.8	3535.7

tributary volume alone is responsible for the contrasting patterns. Instead, differences in discharge, river sinuosity, habitat, stock size, or combinations of these factors may be responsible.

Temporal and spatial overlap in spawning distributions of American shad and striped bass occurs in the York River system but the primary spawning grounds of these species are disjunct. Evidence of spawning and peak egg abundance for both species was apparent throughout the water temperature range of 13–19°C in both rivers. Trends of general abundance for both years and rivers indicated that American shad spawn in regions upstream of striped bass primary spawning grounds (Fig. 4). Trophic interactions, especially predation and competition, may explain the disjunct spawning habitats of these species in the York River. Striped bass may be important predators on American shad in freshwater (Mansueti and Kolb, 1953; Walburg and Nichols[3]). Although recent studies have failed to detect

Table 2

Relative abundance (average density × river volume, numbers × 10^8) and ratios of eggs and larvae of American shad (*Alosa sapidissima*) and striped bass (*Morone saxatilis*) collected in the Mattaponi and Pamunkey rivers, Virginia (1997–99). River volume (10^7 m^3) consists of reaches where eggs (spawning reaches) or larvae (nursery reaches) were found.

	River volume			Larvae		
Species	Spawning reaches	Nursery reaches	Eggs	Yolksac	Postyolksac	Total larvae
American shad						
Mattaponi	6.1	9.4	0.36	0.27	0.63	0.94
Pamunkey	1.9	12.0	0.07	0.13	0.07	0.21
Mattaponi: Pamunkey	3.2	0.8	5.5	2.0	8.8	4.6
Striped bass						
Mattaponi	7.9	3.3	1.6	1.3	2.6	4.0
Pamunkey	12.0	11.0	47.0	29.0	10.0	39.0
Pamunkey: Mattaponi	1.5	3.3	29.0	22.3	3.8	9.9

American shad in the diets of striped bass (Manooch, 1973; Austin and Walter[5]), this absence may be due to current low numbers of American shad in relation to other clupeids. Correspondingly, American shad juveniles have the potential to prey upon striped bass larvae (McGovern and Olney, 1988). Competition for food may occur between the early life stages of these two species as well. According to several studies, larval and juvenile stages of striped bass and American shad feed on similar prey items (Massmann, 1963; Markle and Grant, 1970; Setzler-Hamilton et al., 1981; Gardinier and Hoff, 1982; Crecco and Blake, 1983; Johnson and Dropkin, 1997; Ross et al., 1997). Distinct spawning locations of these species may act to minimize competition between larval- and early juvenile-stage fish, which use nursery locations downriver of spawning reaches. There is also potential overlap in habitat use between the juveniles of these species because both species occupy shallow nearshore waters. Some habitat overlap may be avoided by differing inshore-offshore diel migration patterns. American shad occupy nearshore areas during daylight and move offshore during night hours (Schmidt et al., 1988), whereas striped bass have been observed to predominately occupy nearshore habitats during both day and night hours (Boynton et al., 1981; Rudershausen and Loesch, 2000).

Locations of striped bass spawning grounds on the Pamunkey River in this study corresponded to those of previous studies. Primary spawning reaches on the Pamunkey River were previously reported from 8–48 km above West Point (Rinaldo, 1971); at approximately 27 km (Pamunkey) and 14 km (Mattaponi) above the mouth of each river (Tresselt, 1952); and within the first 40 km of tidal freshwater of both rivers (Grant and Olney, 1991). In the our study, some striped bass eggs were collected on the Pamunkey River upstream of previously reported locations, but in lower abundance than occurred downstream. In the Mattaponi River, striped bass eggs were absent in upstream locations, an observation in agreement with previous surveys (Tresselt, 1952; Rinaldo, 1971; Grant and Olney, 1991; McGovern and Olney, 1996).

On both rivers, American shad were collected in higher abundance upriver of previously reported primary ranges by Massmann (1952). He observed peak egg abundance from 96.2 to 111.0 rkm on the Pamunkey River and from 81.4 to 94.4 rkm on the Mattaponi River. This is in part because we sampled farther upriver than Massmann. However, in those upriver reaches that both studies sampled, eggs were found in higher abundance in 1997–99. Shifting spawning habitats (possibly due to changes in population structure and size, climate, or river discharge), sampling deficiencies, unknown catchability differences between the studies, or some combination of these factors may explain these historical differences. As populations of American shad fluctuate, the spawning area used will likely expand or shrink. If restoration efforts are successful, the availability of suitable spawning areas may become a limiting factor to population growth. Further studies of habitat suitability for spawning within this system are underway to elucidate potential spawning reaches and optimal areas.

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[5] Austin, H. M., and J. F. Walter. 1998. Food habits of large striped bass in the lower Chesapeake Bay and its tributaries March 1997–May 1998. Final report to the Marine Recreational Fisheries Advisory Board and Commercial Fisheries Advisory Board, VMRC, 56 p. Contract number RF-97-08 and CF09709-08. Virginia Institute of Marine Science, Gloucester Point, VA 23062.

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Spawning, growth, and overwintering size of searobins (Triglidae: *Prionotus carolinus* and *P. evolans*)*

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The northern searobin, *Prionotus carolinus*, and striped searobin, *P. evolans*, are among the most common benthic fishes of continental shelf waters between Cape Cod and Cape Hatteras, and both species have contributed occasionally to landings of the U.S. middle Atlantic states. Although several life history studies of these species have been published (Marshall, 1946; Wong, 1968; McEachran and Davis, 1970; Richards et al., 1979; McBride et al., 1998), their early life history has been poorly documented until recently (McBride and Able, 1994; Able and Fahay, 1998; McBride et al., 2002). Obstacles to early life history studies of these searobins include the following: 1) eggs and preflexion larvae are difficult to identify; 2) spawning occurs concurrently for several months; 3) slow growth rates confound analysis of size frequencies for determining cohort structure, and 4) conventional sampling methods have provided few late-stage larvae and early juveniles. I set out to avoid these problems by collecting juvenile specimens from the field and analyzing their otolith microincrements to determine spawning periodicity and growth rates. This approach has not previously been applied to any triglid (Secor et al., 1992).

This study demonstrates both interspecific and intraspecific differences in size during the first year. A literature review also suggests that age-0 *P. carolinus* are smaller than age-0 *P. evolans* and that conspecifics at northern latitudes are larger than conspecifics at southern latitudes (Table 1). In this study, daily sagittal micro-increments were validated and used to test whether interspecific spawning date differences, growth rate differences, or both, are responsible for size differences at first winter. Size at first annulus formation was also examined as an independent measure of age and growth rate. The results of this study improve our understanding of the continental shelf as a nursery ground and the geographic variation in life history traits for these two species.

Materials and methods

Otolith micro-increment validation

Otolith ontogeny was examined by using cultured embryos and yolksac larvae. *Prionotus carolinus* eggs were collected from ripe adults in August 1992 in coastal waters and fertilized in the laboratory. Embryos were raised in 10-liter aquaria under a 12:12 hour light:dark cycle, at 31 ppt salinity, and 26°C. Cultured *P. carolinus* embryos began to hatch after 48 hours and nearly all fish had hatched by 56 hours. Laboratory temperatures unintentionally dropped to 22°C after hatching, but no mortality was observed. Embryos and larvae were preserved in 95% ETOH at 8–16 hour intervals for the first three days and 22–26 hours for the following three days. No fish survived beyond six days. No water was exchanged, but constant aeration kept the aquaria well mixed during the experiment. Newly hatched *Artemia* sp. nauplii were supplied to yolksac larvae, but no feeding was observed. All mortalities appeared to be caused by starvation.

Embryos or larvae were placed on a slide under a cover slip or set in immersion oil (Secor et al., 1992) to examine otolith ontogeny. Otolith presence, size, and development were noted with both a binocular scope (≤50×) and a compound microscope (40–1000×) with polarized light. Notochord length (NL) was measured with an ocular micrometer to the nearest 0.1 mm. Otoliths were measured from a digitized video image through a compound microscope to the nearest 0.001 mm.

Field-collected *P. carolinus* juveniles were chemically marked with tetracycline, held in the laboratory under controlled conditions, and the relationship between "days captive" and "rings after the tetracycline mark" was tested against a 1:1 ratio. Newly settled *P. carolinus* (10–15 mm standard length [SL]) were collected near Beach Haven Ridge (New Jersey) by using a 1- or 2-m beam trawl on five different dates in October 1992 (see McBride et al. [2002] for sampling locations). These fish were divided into four replicate groups; each group was marked separately with a solution of oxytetracycline (dihydrate) and ambient seawater (a concentration of 500 mg/L; 26–28 ppt; 20–22°C) for 24 hours.

One 40-liter aquarium per replicate group was maintained as a flow-through (about 1–10 mL/s) system. Daily water temperature averaged 20.6°C (±2.7 SD), salinity averaged 28.5 ppt (±1.4) and the photoperiod was 12:12 hours of light:dark. Tetracycline-marked fish were fed thawed *Artemia* sp. 2–4 times daily, and a sup-

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Table 1

Standard length (mm) at age for *Prionotus carolinus* and *P. evolans* from two different geographic regions. Fishes older than age 6 are not included because they were typically represented by only individual fishes. nd = no data.

	Chesapeake		New England	
Age (yr)	*P. carolinus*[1]	*P. evolans*[2]	*P. carolinus*[3]	*P. evolans*[3]
0	nd	nd	75	90
1	126	132	130	160
2	163	186	195	210
3	180	207	220	235
4	197	224	245	260
5	204	245	255	290
6	211	270	270	305

[1] Average length values converted from fork length using equations in Wong (1968; Tables 2 and 3).
[2] Values are medians converted from fork lengths as reported in McEachran and Davis (1970, p. 347–348).
[3] Values estimated as a median from Richards et al. (1979; Fig. 7).

plemental feed with vitamins and oils was given at least once each week. Their ration was approximately 10% of their body weight/day; this ration was adjusted 1–3 times weekly to reflect the changes in weight during the experiment. Uneaten food was removed daily. Three to seven fish were removed from each replicate aquarium after 16, 26, 36, 46 days (total n=75), measured to the nearest 0.1 mm SL, and preserved in 95% ETOH. Growth rates between the replicate tanks varied from 0.21 to 0.44 mm/d according to least squares, linear regression of standard length on date of removal. Eleven of 86 fish initially placed in the aquaria died during the experiment and were not used for validating microincrement deposition rate.

After preservation, both sagittae were extracted from each fish, mounted on a coded glass slide in nail polish, sanded along the sagittal plane, and swabbed with immersion oil. After a fluorescing increment was located in the ocular crosshairs using a ultraviolet light source, the light was turned off and I counted the microincrements from the crosshair to the otolith margin on three separate dates. An average of these three counts was used to estimate increment number from the tetracycline mark to the peripheral edge.

Daily age and growth

Sagittal microincrements were examined from other postsettlement *P. carolinus* and *P. evolans* juveniles collected during August–October 1991 at locations in Great Bay (New Jersey), Delaware Bay, and continental shelf sites between Chesapeake Bay and Long Island Sound. Fishes were collected with bottom trawls and seine nets and either preserved in 95% ETOH or frozen. Specimens for aging were subsampled in a stratified (1-mm length category) random manner to proportionally represent the complete size range of each independent sample.

Otoliths were mounted on coded slides in nail polish and sanded to the core along one side of the sagittal plane or embedded in an epoxy resin and sectioned to the core (Secor et al., 1992). I counted microincrements through a compound microscope, typically at 400× by using polarized light, on three separate occasions. If the range of all three counts was >20% of the mean count, then the specimen was excluded from further analyses; this criterium resulted in 14 of 137 specimens being rejected. The mean increment count for sagittae was used to estimate "otolith age" in days. Daily age included four additional days—an estimate of the time between hatching and the date of first ring deposition. Hatching dates were calculated by subtracting daily age from date of capture.

Annual age and growth

Size attained by the end of the first growing season was estimated from *P. carolinus* and *P. evolans* juveniles collected during later winter and early spring cruises by the National Oceanic and Atmospheric Administration's National Marine Fisheries Service (see also McBride et al., 1998). Fishes were sampled with bottom trawls during two consecutive cruises (February 1993 and March–April 1993), which included a total of 447 stations (Fig. 1). The effective period of sampling for searobins was actually February–March (only one searobin was caught in 160 tows made during April).

At sea, only fishes ≤120 mm SL were saved because larger fishes were presumed to be older than 1 year (see Richards et al., 1979). Fishes were kept frozen to preserve the otolith structure. Specimens were subsampled from each independent sample (i.e. tow) in a stratified (5-mm length intervals), random manner. This subsampling approach was chosen again to moderate the resulting sample size while proportionally representing the complete size range of each independent sample; this approach also exaggerates the size range by dampening the modes of resulting size-frequency data. Sagittae were mounted in nail polish on a coded glass slide, sanded, and polished along

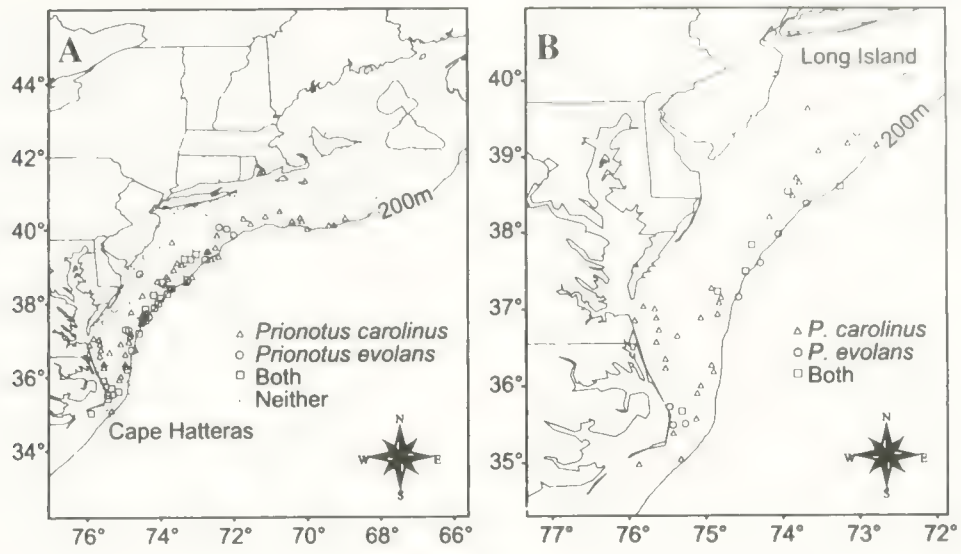

Figure 1

(**A**) Locations of all sampling during February–April 1993. Locations are indicated where searobins were and were not collected in tows. (**B**) Sample locations for age-0 searobins used for estimating overwintering size. Locations are for cruise dates during February–March 1993. No age-0 *Prionotus* spp. were collected during April 1993, and sampling areas covered during April (north of 40°N) are not shown.

the sagittal plane, and viewed under a binocular scope (typically at 20×) to check for the presence (e.g. age-1) or absence (e.g. age-0) of an annulus. Annulus formation occurs in March for both species (Wong, 1968; McEachran and Davis, 1970), and an annulus on the otolith margin was not counted.

Results and discussion

Otolith microstructure

Two pairs of otoliths (the sagittae and lapilli) were present prior to hatching in cultured embryos, having formed at the same time as the optic vesicles. No asterisci were observed in cultured yolksac larvae and, from personal observations of field-caught specimens, the asterisci form after flexion of the notochord. First ring deposition in sagittae was contemporaneous with eye pigmentation and yolksac absorption, although this process was not observed directly. Instead, it was observed that the diameter of the sagittal core (=primordium) steadily increased during yolksac absorption but that no microincrements were evident. I conclude that the laboratory specimens would have laid down their first ring at yolk absorption had they survived because the diameters of their sagittae were similar to the sagittal core diameters of wild fish (i.e. the diameter of the first microincrement). The maximum sagittal diameter of laboratory-cultured *P. carolinus* larvae was 26.3 µm and the mean sagittal core diameter of field-caught fish was 27.0 or 26.8 µm (n=8 flexion stage and n=6 postflexion specimens, respectively).

Yolksac absorption occurred approximately six days after fertilization and four days after hatching at 22–26°C; therefore four days were added to the average number of microincrements counted for both species, although this developmental pattern was observed only for *P. carolinus*. The rate of larval development observed in the present study is consistent with other reports of *P. carolinus* cultured at 15–22°C. Yuschak and Lund (1984) observed yolksac absorption by *P. carolinus* larvae at 3.4 mm NL and first feeding at 3.5–5 days after hatching. Kuntz and Radcliffe (1917) reported *P. carolinus* hatching at about 60 hours (2.5 days) and starvation 5–6 days after hatching.

Sagittal microincrement deposition occurred daily in chemically marked *P. carolinus* juveniles cultured in the laboratory. Data from four replicate aquaria (75 fish) were pooled because an ANCOVA did not indicate a significant difference by either the interaction of treatments (slope–replicate interaction: P=0.48) or the covariate (replicate: P=0.12). The resulting relationship was

$$Y = 1.23 + 0.94\ (X),$$

where Y = the number of microincrements after the tetracycline mark; and
X = the number of days following marking.

A test of statistical power (i.e. 1 – beta, as in Dixon and Massey [1951] and Cohen and Cohen [1975]) indicated a 99.9% confidence that microincrement deposition did not deviate from unity by more than 0.02 rings/d. McBride (1994) presented preliminary evidence of daily sagittal microincrements in *P. evolans*.

Reproductive seasonality The reproductive period for both species was prolonged and overlapping (Fig. 2). The range of *P. carolinus* hatching dates was from 19 May to 5 September and *P. evolans* hatching dates extended from 2 June to 3 September. Median hatching dates for *P. carolinus* were significantly later than *P. evolans* (13 August versus 26 July; Wilcoxon 2-sample test: P=0.011). Both species spawned for at least three months but *P. carolinus* hatching dates were dramatically skewed to the left (i.e. most individuals hatched late in the season). Previous studies independently demonstrated that both species spawn contemporaneously in the New York Bight: Keirans et al. (1986) calculated egg densities, Wilk et al. (1990) examined gonadosomatic indices, McBride and Able (1994) used length-frequency analysis, and McBride et al. (2002) examined larval densities. All demonstrated an extended spawning season for both species from about May to September; furthermore, a bimodal pattern of spawning output was reported for *Prionotus* spp. by Keirans et al. (1986) and McBride and Able (1994). My sampling procedure (i.e. a stratified, random design with respect to length intervals) would flatten frequency peaks and emphasize the range of hatching dates, a method not well suited for identifying multiple spawning peaks. Moreover, McBride et al. (2002) identified notable geographic variation in spawning seasonality, which could not be separated out in the present study and should be accounted for in future research. Intra-annual reproductive periodicity of *Prionotus* should also be evaluated by examining gonads for cyclic, group-synchronous oocyte development, which could be an underlying process leading to a protracted spawning period with regularly spaced peaks in production.

I conclude that interspecific size differences are at least partly the result of interspecific differences in reproductive seasonality (Table 1; i.e. the smaller congener was spawned later in the year). However, Able and Fahay (1998) noted that *P. evolans* eggs are larger than *P. carolinus* eggs; thus size differences exist among embryos. In addition, McBride et al. (2002) showed that interspecific size-at-age differences are evident throughout the larval period.

Age and growth Age-0 *P. evolans* were larger at a common age than *P. carolinus* (Fig. 3). On the basis of all individuals examined, *P. evolans* did not grow at a significantly higher rate (ANCOVA interaction of slopes; P=0.099), but this species was significantly larger than *P. carolinus* in general (ANCOVA test of intercepts; P=0.0001). The regression slopes, based on all data, were significantly different from zero (P<0.001) for both *P. carolinus* (SL=0.12+0.323×*age*; r^2=0.62; n=70) and *P. evolans* (SL=3.52+0.429×*age*; r^2=0.53; n=53). The intercepts for these linear growth models were biologically meaningful, particularly that for *P. evolans* because the intercept was roughly equal to the known size at hatching (3 mm; Able and Fahay, 1998). *Prionotus evolans* collected at four different stations in Delaware Bay during October 1991 deviated strongly from the average growth rates for this species (Fig. 3). Such small, slow-growing fish demonstrated the degree of intraspecific variation possible for *P. evolans* growth rates.

Age-0 *P. carolinus* were also much smaller on average than *P. evolans* during winter (Fig. 4). By February–March, age-0 *P. carolinus* ranged from 27 to at least 117 mm SL, but this size distribution was strongly bimodal with modes at 42.5 mm and 87.5 mm SL. The age-0 *P. evolans* were all larger than 75 mm SL and appeared to grow even larger than 120 mm SL, which was the cutoff size for collections, so that the interspecific size difference is even greater than that indicated in Figure 4. Apparently all age-1 *P. evolans* are larger than this cutoff value because none were observed in the samples, whereas age-1 *P. carolinus* ranged from 56 to at least 118 mm. Although age-1 *P. carolinus* were generally larger than age-0 conspecifics, the sizes of both age classes overlapped in a manner that would confound length–frequency analyses of this species.

The intraspecific size variation of age-0 fishes, of both *Prionotus* species, was spatially correlated. Individually,

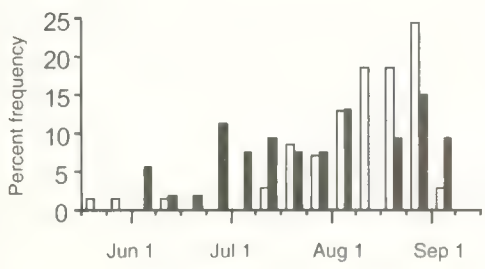

Figure 2

Backcalculated hatching dates (*date of capture* – [*otolith age* + 4]) for age-0 *Prionotus carolinus* (open bars; n=70) and *P. evolans* (filled bars; n=53) collected in estuarine and continental shelf habitats during 1991.

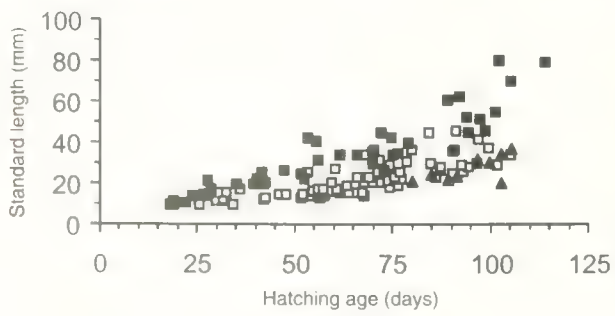

Figure 3

Length-at-age relationships for *Prionotus carolinus* (open symbols) and *P. evolans* (filled symbols). *Prionotus evolans* from Delaware Bay are depicted separately (triangles) from all other *P. evolans* (squares). Sample sizes are identical to those in Figure 2.

depth and latitude explained a significant ($r^2 \geq 0.30$; $P < 0.01$) amount of the variability of the mean size of age-0 *P. carolinus* during winter (Fig. 5). Each variable also contributed significantly ($P \leq 0.02$) to a multiple regression; nearly half ($r^2 = 0.47$) of the variance of the mean age-0 *P. carolinus* size between individual trawl tows was explained by the linear, least-squares equation

$$mean\ SL = -158 + 0.37 \times (depth[\text{m}]) + 5.7 \times (latitude[^\circ\text{N}]).$$

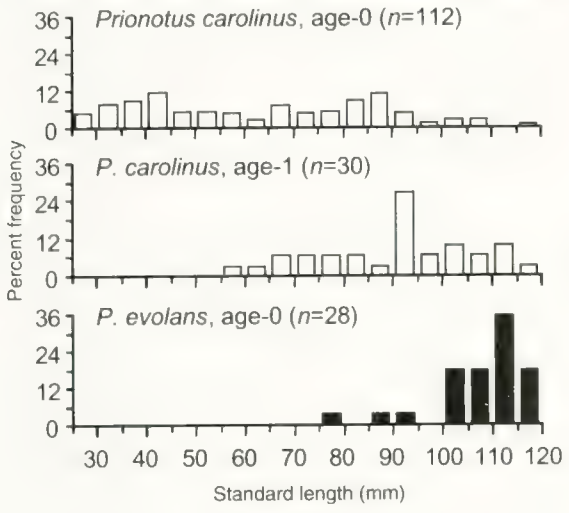

Figure 4

Size frequency of *Prionotus carolinus* (open bars) and *P. evolans* (filled bars) based on collections from continental shelf habitats in February–March 1993 (see Figure 1B). The upper boundary (120 mm SL) represents the size cutoff used during field collecting and does not necessarily define the maximum size attained for any age class. *n* = number of fish in sample.

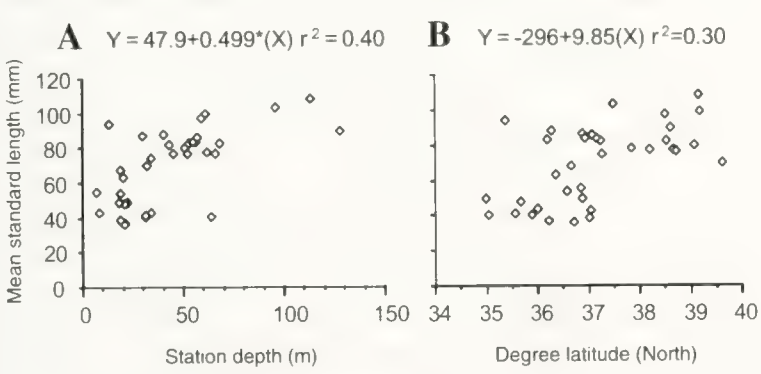

Figure 5

Linear relationships between mean size (standard length [mm]) of age-0 *Prionotus carolinus* and depth (**A**) or latitude (**B**) of sampling location. All fish were collected during February–March 1993 with bottom trawls in continental shelf waters (see Fig. 1B). See text for further details of multivariate analysis and results.

Similar analyses for *P. evolans* suggested that depth, but not latitude, was correlated with age-0 size variations. However, samples sizes of *P. evolans* were smaller than those for *P. carolinus* and age-0 *P. evolans* grow larger than the maximum size saved in field collections; therefore it is possible that age-0 *P. evolans* have a similar response to depth and latitude as age-0 *P. carolinus*.

Life history consequences

Late-summer spawning by *Prionotus* is not unique among fishes in waters offshore of the middle Atlantic states: *Scophthalmus aquosus* spawn late in the summer (Morse and Able, 1995) and three hake species (*Urophycis bilinearis*, *U. chuss*, and *U. regia*) have peaks in spawning during July–September (Wilk et al., 1990). Late spawning is not even evident for all *Prionotus* throughout their range. McBride et al. (2002) noted that the reproductive season for *Prionotus* varies with respect to latitude and coastal depth, and their observation that late spawning was common only offshore of the southern middle Atlantic states is consistent with the data presented in the present study for larger (i.e. presumably older) *P. carolinus* found during winter at higher latitudes. Sherman et al. (1984) noted a close association between *Prionotus* spawning cycles and zooplankton abundance cycles in continental shelf waters, and they suggested that the *Prionotus* spawning season is adapted for larvae to experience optimal prey encounter rates. However advantageous this match between larvae and their prey may seem, late-spawned *Prionotus* have an apparent size disadvantage during winter compared to many other species because of a shorter growing season.

Generally, coastal fishes of temperate waters appear to spawn in a manner that maximizes growth rates and size of their progeny, particularly in response to size-selective mortality (Conover, 1992; Sogard, 1997). Overwintering sizes of age-0 *P. carolinus*, however, do not suggest that such a scenario is occurring. Age-0 *P. carolinus* are smaller than or about the same size as typical age-0 prey species on the continental shelf, such as *Menidia menidia* and *Anchoa mitchilli* (Conover and Murawski, 1982; Vouglitois et al., 1987). Despite their small size, reports of age-0 *Prionotus* in gut contents of predatory fishes are rare (Marshall, 1946; Richards et al., 1979; Maurer and Bowman[1]). Size-selective mortality, a process that would select for early spawning and fast growth rates, may not be important because *Prionotus* are capable of burying themselves in the substrate (Bardach and Case, 1965)—an antipredator tactic. If size-selective mortality is not important, then

[1] Maurer, R. O., Jr., and R. E. Bowman. 1975. Food habits of marine fishes of the northwest Atlantic–data report. Laboratory Reference 75-3, 90 p. Northeast Fisheries Science Center. Woods Hole, MA 02543.

it is possible that overwinter mortality rates are similar between small individuals spawned late in the growing season and larger conspecifics spawned early, and that late spawning is not selected against for *P. carolinus*.

In this study, I demonstrate that interspecific and clinal variations of overwintering size for *Prionotus* species exist and that these are consistent with previous age and growth studies. Ginsburg (1950) also noted clinal variation for some meristic characters of both congeners that is consistent with Jordan's rule (i.e. higher counts at higher latitudes). McBride et al. (2002) have demonstrated regional differences in spawning seasonality for *Prionotus* species and short larval durations that limit dispersal of *Prionotus* planktonic stages; these are the likely mechanisms maintaining regional differences in juvenile sizes and meristic characters. Researchers should be aware of this demonstrated clinal variation and the potential for further life history, phenotypic, and possibly genetic variation of *Prionotus* species in temperate waters of the western North Atlantic.

Acknowledgments

K. Able, R. Cowen, M. Fahay, J. P. Grassle, R. Loveland, and C. L. Smith contributed helpful comments on an earlier draft and thoughtful discussions regarding this research. D. Flescher and J. Galbraith provided data and specimens from bottom trawl collections by the National Marine Fisheries Service. D. Byrne (NJ) and S. Michels (DE) provided data and specimens from the bottom trawl surveys by their respective state agencies. L. S. Hales improved the quality of the culturing experiments. L. S. Hales, D. Merryman, and H. Patterson assisted with otolith preparation. M. Palavido prepared the maps in Figure 1. This study was part of a doctoral dissertation (R.S.M.) and was funded by the Institute of Marine and Coastal Sciences (IMCS-Rutgers) and the NOAA National Undersea Research Program for the New York Bight. Final preparation and revision of this manuscript were made at the Florida Marine Research Institute. I thank all of the above.

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Errata

Erratum 1

***Fishery Bulletin* 100(2): 242.**

Kitada, Shuichi, and Kiyoshi Tezuka.

Longitudinal logbook survey designs for estimating recreational fishery catch, with application to ayu (*Plecoglosssus altivelis*)

Please note that in the printed copies some equations in Appendix 1 and Appendix 2 incorrectly show carets over the word "Cov."

Appendix 1 and Appendix 2 (page 242) should read as follows:

Appendix 1: The covariance of two estimators from sample means

First we consider the covariance of two total estimates. Let X_i and Y_i be simple random samples (i=1, . . . , n) from a population of size N with mean μ_x and μ_y, and $\overline{X}$ and $\overline{Y}$ be two sample means.

Cochran (1977, p .25) derived the covariance of two-sample mean, that is

$$\begin{aligned}\mathrm{Cov}(\overline{X},\overline{Y}) &= \frac{N-n}{N}\frac{1}{n}\mathrm{Cov}(X,Y)\\ &= \frac{N-n}{N^2 n}\sum_{i=1}^{N}(X_i-\mu_x)(Y_i-\mu_u).\end{aligned}$$

This is estimated by

$$\begin{aligned}\widehat{\mathrm{Cov}}(\overline{X},\overline{Y}) &= \frac{N-n}{N}\frac{1}{n}\widehat{\mathrm{Cov}}(X,Y)\\ &= \frac{N-n}{Nn(n-1)}\sum_{i=1}^{n}(X_i-\overline{X})(Y_i-\overline{Y}).\end{aligned}$$

The covariance between two population total estimators is defined by

$$\begin{aligned}\mathrm{Cov}(\hat{X},\hat{Y}) &= \mathrm{Cov}(N\overline{X},N\overline{Y}) = E(N\overline{X}-N\mu_x)(N\overline{Y}-N\mu_y)\\ &= N^2\mathrm{Cov}(\overline{X},\overline{Y}) = \frac{N(N-n)}{n}\mathrm{Cov}(X,Y).\end{aligned}$$

This is estimated by

$$\widehat{\mathrm{Cov}}(\hat{X},\hat{Y}) = \frac{N(N-n)}{n(n-1)}\sum_{i=1}^{n}(X_i-\overline{X})(Y_i-\overline{Y}).$$

For the monthly total catches, we get

$$\widehat{\mathrm{Cov}}(\hat{C}_k^{(s)},\hat{C}_{k'}^{(s)}) = \frac{N(N-n)}{n(n-1)}\sum_{i=1}^{n}(C_{ik}-\hat{\overline{C}}_k)(C_{ik'}-\hat{\overline{C}}_{k'}).$$

Appendix 2: Approximate covariance between $\hat{W}_k^{(s)}$ and $\hat{W}_{k'}^{(s)}$

Taylor's series of $\hat{W}_k$ with respect to the random variables is obtained by

$$\hat{W}_k = C_k\overline{w}_k + \overline{w}_k(\hat{C}_k - C_k) + C_k(\hat{\overline{w}}_k - \overline{w}_k).$$

From Taylor's series (mentioned above), the approximate covariance is obtained.

$$\begin{aligned}\mathrm{Cov}(\hat{W}_k^{(s)},\hat{W}_{k'}^{(s)}) &= E(\hat{W}_k^{(s)}-W_k^{(s)})(\hat{W}_{k'}^{(s)}-W_{k'}^{(s)})\\ &= E\left[\overline{w}_k(\hat{C}_k^{(s)}-C_k^{(s)})+C_k^{(s)}(\hat{\overline{w}}_k-\overline{w}_k)\right]\\ &\quad\left[\overline{w}_{k'}(\hat{C}_{k'}^{(s)}-C_{k'}^{(s)})+C_{k'}^{(s)}(\hat{\overline{w}}_{k'}-\overline{w}_{k'})\right]\\ &= \overline{w}_k\overline{w}_{k'}\mathrm{Cov}(\hat{C}_k^{(s)},\hat{C}_{k'}^{(s)})+\overline{w}_kC_{k'}^{(s)}\mathrm{Cov}(C_k^{(s)},\hat{\overline{w}}_{k'})\\ &\quad+C_k^{(s)}\overline{w}_{k'}\mathrm{Cov}(\hat{\overline{w}}_k,\hat{C}_{k'}^{(s)})+C_k^{(s)}C_{k'}^{(s)}\mathrm{Cov}(\hat{\overline{w}}_k,\hat{\overline{w}}_{k'}).\end{aligned}$$

Here $\hat{C}_{(\cdot)}^{(s)}$ and $\hat{\overline{w}}_{(\cdot)}$ are independent, and both w_k and $w_{k'}$ are estimated from different samples. Therefore Cov $(\hat{C}_k^{(s)},\overline{w}_{k'}) = \mathrm{Cov}(\hat{\overline{w}}_k,C_{k'}^{(s)}) = \mathrm{Cov}(\hat{\overline{w}}_k,\hat{\overline{w}}_{k'}) = 0$, then we get the covariance as only the first term.

Erratum 2

***Fishery Bulletin* 100 (2):258.**

McFee, Wayne E., and Sally R. Hopkins-Murphy

Bottlenose dolphin (*Tursiops truncatus*) strandings in South Carolina, 1992–1996

Last sentence of abstract should read as follows:

Incidents of bottlenose dolphin rope entanglements accounted for 16 of these cases.

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Fishery Bulletin

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Hybridization between two serranids, the coney (*Cephalopholis fulva*) and the creole-fish (*Paranthias furcifer*), at Bermuda*

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Abstract—Intergeneric hybridization between the epinepheline serranids *Cephalopholis fulva* and *Paranthias furcifer* in waters off Bermuda was investigated by using morphological and molecular characters. Putative hybrids, as well as members of each presumed parent species, were analyzed for 44 morphological characters and screened for genetic variation at 16 nuclear allozyme loci, two nuclear (n)DNA loci, and three mitochondrial (mt)DNA gene regions. Four of 16 allozyme loci, creatine kinase (*CK-B**), fumarase (*FH**), isocitrate dehydrogenase (*ICDH-S**), and lactate dehydrogenase (*LDH-B**), were unique in *C. fulva* and *P. furcifer*. Restriction fragments of two nuclear DNA intron regions, an actin gene intron and the second intron in the S7 ribosomal protein gene, also exhibited consistent differences between the two presumed parent species. Restriction fragments of three mtDNA regions—ND4, ATPase 6, and 12S/16S ribosomal RNA—were analyzed to identify maternal parentage of putative hybrids. Both morphological data and nuclear genetic data were found to be consistent with the hypothesis that the putative hybrids were the result of interbreeding between *C. fulva* and *P. furcifer*. Mean values of 38 morphological characters were different between presumed parent species, and putative hybrids were intermediate to presumed parent species for 33 of these characters. A principal component analysis of the morphological and meristic data was also consistent with hybridization between *C. fulva* and *P. furcifer*. Thirteen of 15 putative hybrids were heterozygous at all diagnostic nuclear loci, consistent with F_1 hybrids. Two putative hybrids were identified as post-F_1 hybrids based on homozygosity at one nuclear locus each. Mitochondrial DNA analysis showed that the maternal parent of all putative hybrid individuals was *C. fulva*. A survey of nuclear and mitochondrial loci of 57 *C. fulva* and 37 *P. furcifer* from Bermuda revealed no evidence of introgression between the parent species mediated by hybridization.

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Poey (1860, 1875) described the genus *Menephorus* for two species, *M. dubius* Poey, 1860 and *M. punctiferus* Poey, 1875, each based on a single specimen of grouper that appeared to be intermediate in morphology between the coney, *Cephalopholis fulva* and the creole-fish, *Paranthias furcifer*. Smith (1966) analyzed Poey's specimens for 45 meristic and morphometric characters and found the specimens to be intermediate to *P. furcifer* and *C. fulva* for 40 of these characters—results consistent with intergeneric hybridization. Smith (1966) also noted that *P. furcifer* may be more closely related to the epinepheline serranids (such as *C. fulva*) than previously thought. Interest in this possible case of intergeneric hybridization was renewed in 1993 when Bermudian ichthyology student James Parris Jr. asked one of the authors if he would be interested in a specimen his father caught that "had the head of a coney and the tail of a barber (creole-fish)." Since that time several other putative hybrids have been caught off Bermuda (Smith-Vaniz et al., 1999), and we have initiated a program to collect putative hybrids from local fishermen to further investigate this phenomenon.

The presumed parents of the putative hybrids are members of different serranid genera that have strikingly different morphologies, occupy different ecological niches, and have different behaviors (Heemstra and Randall, 1993; Smith, 1966). The major distinguishing features of *P. furcifer* are its forked

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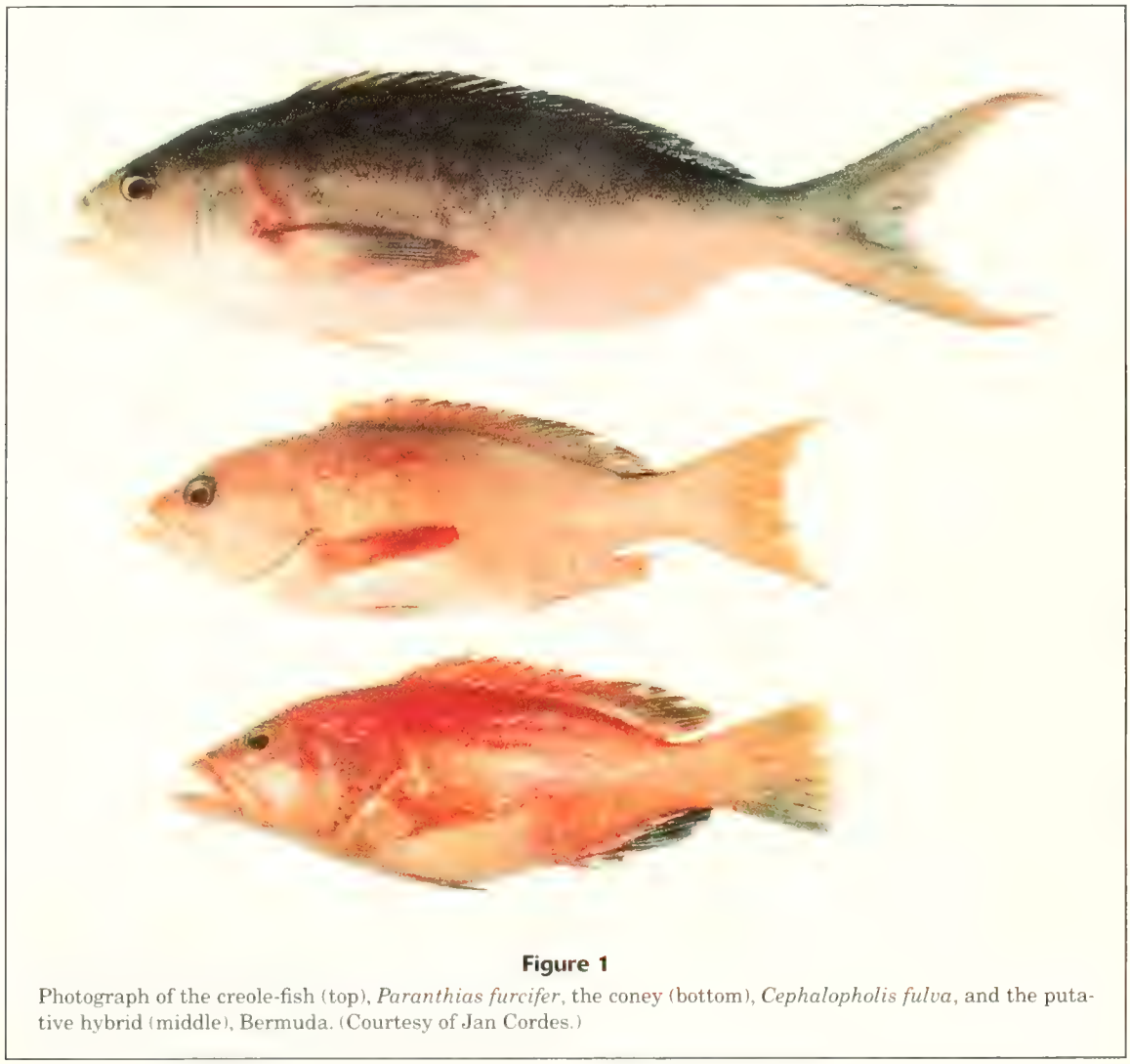

Figure 1

Photograph of the creole-fish (top), *Paranthias furcifer*, the coney (bottom), *Cephalopholis fulva*, and the putative hybrid (middle), Bermuda. (Courtesy of Jan Cordes.)

caudal fin and the size and shape of its mouth (Fig. 1). *Paranthias furcifer* is dark red in color; darker dorsally, lightening ventrally (Heemstra and Randall, 1993). There is an orange spot at the upper end of the base of the pectoral fin and three white spots dorsal to the lateral line. Bermuda is the northern limit of the distribution of *P. furcifer* in the western Atlantic and the species occurs throughout the Bahamas and Antilles and along the American coast from the Gulf of Mexico south to Brazil (Smith, 1971; Smith-Vaniz et al., 1999).

In contrast, *C. fulva* is usually scarlet in color and covered with light blue-green spots, each surrounded by a black ring (Heemstra and Randall, 1993). There are two black spots on the edge of the lower jaw as well as on top of the caudal peduncle. *Cephalopholis fulva* has rounded caudal, anal, and dorsal fins, similar to fins of other epinepheline serranids (Heemstra and Randall, 1993) (Fig. 1). In the northwestern Atlantic, *C. fulva* has a distribution similar to that of *P. furcifer*; it occurs as far north as Bermuda, throughout the Bahamas, Antilles, and along the east coast of the Americas from South Carolina to Brazil (Heemstra and Randall, 1993; Smith, 1971; Smith-Vaniz et al., 1999).

Morphologically, the putative hybrids are almost exactly intermediate to the parent species (Fig. 1). In his 1966 review, Smith noted that the hybrids have some characters unique to *C. fulva* and *P. furcifer*. For example, the putative hybrid individuals have both a moderately forked tail and blue spots surrounded by a black ring. *Paranthias furcifer* is the only Atlantic grouper with a forked tail suggesting that it is one of the putative parents and *C. fulva* is the only Atlantic grouper that has blue spots with a black ring. Presence of both traits together in a single individual strongly suggests interbreeding between the two species. The geographic extent of the putative hybrid is not well known; however specimens exist from Cuba and Bermuda (Smith-Vaniz et al., 1999), and it has been reported from Jamaica (Thompson and Munro, 1978).

Hybridization has traditionally been detected by using morphological characters, but increasingly, genetic analyses have also been used for this purpose. Allozyme electrophoresis provides a rapid and cost-effective method to

assess hybridization (Campton, 1987). Through the analysis of multiple loci it is possible to identify F_1 and post-F_1 hybrids, as well as to detect the introgression of alleles between species by hybrid backcrossing. It became evident however, that analysis of nuclear DNA loci is necessary in studies of hybridization as a means to overcome some of the sampling restrictions of allozyme analysis and to provide a survey of biparentally inherited genes (Verspoor and Hammar, 1991). Mitochondrial DNA (mtDNA) has also been used extensively in studies of hybridization. Because mtDNA is maternally inherited in fishes, analysis of the molecule allows one to identify the maternal parent of F_1 hybrids, as well as the sexual preferences of F_1 hybrids and their offspring (Dowling et al., 1996).

The key to using molecular markers to identify hybridization is to find multiple independent nuclear loci and a mitochondrial gene region that have unique alleles in each putative parent species (Dowling et al., 1996). An F_1 hybrid would be heterozygous at all nuclear loci and have a mitochondrial haplotype identical to one parent species (Campton, 1987; Dowling et al., 1989). A backcrossed individual would be heterozygous at some diagnostic nuclear loci and homozygous at others. Therefore the power of demonstrating an F_1 hybrid, as opposed to a backcross or pure parent individual, increases with the number of nuclear loci examined.

In this study, genetic information from four diagnostic allozyme loci, two diagnostic nuclear DNA loci, and three diagnostic mtDNA gene regions, was used to assess hybridization and introgression between *Cephalopholis fulva* and *Paranthias furcifer* in Bermuda waters.

Materials and methods

A total of 51 *Cephalopholis fulva* (Linnaeus, 1758), three *C. cruentata* (Lacepède, 1802), and 37 *Paranthias furcifer* (Valenciennes, 1828) were collected from Bermuda with baited handlines or rotenone solution. In addition, six *C. fulva* and two *C. cruentata* were sampled from Navassa Island. Fifteen putative hybrids were captured by Bermudian fishermen using handlines or lobster traps. *Cephalopholis cruentata* was in-cluded in the study as a possible parent species of the putative hybrid and three *Epinephelus guttatus* (Linnaeus, 1758) specimens from Lee Stocking Island, Bahamas, were used in the preliminary mitochondrial DNA study.

Specimens were frozen upon capture and stored at –20°C or –80°C and transported to the laboratory for analysis. For mitochondrial and nuclear DNA analysis, muscle tissues were removed and placed in storage buffer (0.25M EDTA, 20% DMSO and saturated with NaCl). For allozyme analysis, 1.5-cm^3 pieces of liver and muscle tissue were separately homogenized in 250 µL of chilled (4°C) grinding buffer (0.1 M Tris, 0.9 mM EDTA, and 0.05 mM $NADP^+$, pH 7.2). Samples were centrifuged for 3 min at 16,000 ×g and stored at –80°C or analyzed immediately.

Genomic DNA was isolated from a 1.0-cm^3 piece of muscle tissue by using the phenol/chloroform protocol of Winnepenninckx et al. (1993) with the following modifications. CTAB (hexadecyltrimethylammonium bromide) was not added to the extraction and phenol was added immediately following incubation of the tissue at 37°C. DNA was precipitated by the addition of 0.04 volume of 5M NaCl and 1.0 volume of isopropanol. DNA was resuspended in 150 µL of sterile 0.1X TE (Tris-EDTA) and stored at –20°C.

Table 1

National Museum of Natural History (USNM) and Virginia Institute of Marine Science (VIMS) catalogue numbers for specimens used in the morphological analysis.

Species	Collection	Specimen	Standard length (mm)
C. fulva	USNM	88717	232
	USNM	53134	217
	USNM	53134	176
	USNM	133689	171
	VIMS	10413	222
	VIMS	10414	213
	VIMS	10415	210
	VIMS	10416	170
	VIMS	10417	146
	USNM	320539	240
P. furcifer	VIMS	10410	274
	VIMS	10411	259
	VIMS	10412	274
	USNM	107108	218
	USNM	358541	237
	USNM	33255	207
	USNM	12540	185
	USNM	65605-8244	201
	USNM	65605-8246	176
	USNM	65605-8246	129
Putative hybrid	VIMS	10403	190
	VIMS	10402	199
	VIMS	10401	222
	VIMS	10404	237
	VIMS	10405	210
	VIMS	10406	195
	VIMS	10407	172
	VIMS	10408	114
	VIMS	10409	181
	USNM	1240011	230

Morphological analyses

Specimens of *C. fulva* and *P. furcifer* used in the morphological analysis were obtained from and measured at the National Museum of Natural History (Table 1). Ten putative hybrids were suitable for morphological analysis. The remaining five samples were not properly preserved and morphological analysis was not possible. Hybrid specimens as well as a small number of the *C. fulva* and *P. furcifer* were frozen. Specimens obtained from the National Museum of Natural History were fixed in for-

malin. Morphometric and meristic characters were examined as described in Smith (1971) by using dial calipers and a meter stick. The morphometric data were analyzed by using a sheared principal component analysis with a covariance matrix to confine the effect of size to the first principal component (Humphries et al., 1981; Bookstein et al., 1985; Stauffer et al., 1997). The meristic data were analyzed by using a principal component analysis with a correlation matrix.

Allozyme analysis

Horizontal starch gel electrophoresis followed the protocols described in Murphy et al. (1996). Gels (12%w/v; Starch Art Corp., Smithville, TX) were run on one of three buffer systems: Tris-citrate II buffer (TC II) (30 mAmps for 14 hours), lithium hydroxide buffer (LIOH) (25 mAmps for 14 hours), or Tris borate-EDTA buffer (EBT) (30 mAmps for 14 hours). Histochemical staining followed the protocols of Murphy et al. (1996), and locus nomenclature and allelic designations followed Shaklee et al. (1990).

A preliminary survey of 16 loci in 15 individuals each of *C. fulva* and *P. furcifer* (Table 2) was performed to identify those loci for which the alleles were consistently different among the presumed parent species, *C. fulva* and *P. furcifer*. All parent individuals and putative hybrids were then surveyed for all loci that demonstrated differences between the species.

Nuclear DNA analysis

An actin gene intron and the second intron in the S7 ribosomal protein gene (Chow and Hazama, 1998) were investigated by using restriction fragment length polymorphism (RFLP) analysis. Amplification primers and reaction conditions are listed in Table 3. The regions were amplified by using the PCR reagent system (GIBCO/BRL Life Technologies®, Bethesda, MD) and a 25-µL reaction cocktail (1X PCR buffer with $MgCl_2$, 0.2 mM dNTP, 0.5 µM primer, 2.5 U of *Taq* DNA polymerase, and 25–50 ng genomic DNA template). Some PCR reactions were performed with Platinum® *Taq* high fidelity (GIBCO/BRL Life Technologies®) with a 25-µL reaction cocktail (1X high fidelity buffer, 2 mM $MgSO_4$, 0.2 mM dNTP, 0.2 µM primer, and 2.5 U of Platinum® *Taq* DNA polymerase high fidelity). In other cases, 1 µL dimethyl sulfoxide (DMSO, Fisher Scientific BP231-1, Pittsburgh, PA) was added to the reaction to increase sensitivity.

The amplification products from two individuals of each species for both loci were digested with a panel of restriction enzymes to identify those that exhibited differences between the putative parent species. All samples were subsequently digested with those enzymes that demonstrated differences in the pilot study (Table 3). Digestion reactions (1.5-µL 10X buffer, 3 U restriction enzyme, and 4-µL PCR product) were incubated 2 to 18 hours at 37°C. Digestion products were separated on 2.5% agarose gels (1.25% Ultrapure Agarose, GIBCO/BRL Life Technology (R) + 1.25% NuSieve GTG (R) agarose, FMC Biochemical, Rockland, ME), stained with ethidium bromide and visualized under UV light.

Table 2

Allozyme analysis: information includes loci, buffer systems, and tissues.

Locus	Buffer	Tissue
Alcohol dehydrogenase (*ADH-1** 1.1.1.1)	EBT	liver
Creatine kinase (*CK-B** 2.7.3.2)	LIOH	liver
Creatine kinase (*CK-C**2.7.3.2)	LIOH	liver
Esterase, (*EST-1** 3.1.1.1)	EBT	liver
Esterase, (*EST-2** 3.1.1.1)	EBT	liver
Fumarase, (*FH** 4.2.1.2)	TCII	liver
Glucosephosphate isomerase (*GPI-A** 1.1.1.49)	EBT	liver
Isocitrate dehydrogenase (*ICDH-S** 1.1.1.42)	TCII	liver
Lactate dehydrogenase (*LDH-A** 1.1.1.27)	TCII	muscle
Lactate dehydrogenase (*LDH-B** 1.1.1.27)	TCII	liver
Malate dehydrogenase (*MDH-A** 1.1.1.37)	EBT	muscle
Malate dehydrogenase (*MDH-B** 1.1.1.37)	EBT	muscle
Peptidase-B (*PEP-1** 3.4.11)	LIOH	liver
Peptidase-S (*PEP-2** 3.4.11)	LIOH	liver
Peptidase-C (*PEP-3** 3.4.11)	LIOH	liver
Xanthine dehydrogenase (*XDH** 1.1.1.204)	EBT	liver

MtDNA analysis

The following regions of the mitochondrial genome were surveyed in the three putative parent species and hybrids; the adenosine 5′-triphosphatase subunit 6 (ATPase 6) gene, the 12S/16S ribosomal RNA gene region, and the nicotinamide dehydrogenase subunit 4 (ND4) gene. Amplification primers and reaction conditions are listed in Table 3. Amplified products of two individuals of each putative parent species were screened with restriction enzymes to identify potential differences between *C. fulva* and *P. furcifer* (Table 3). All individuals were screened at the three regions with those enzymes that revealed differences in the preliminary study. Restriction digestion reactions were performed and visualized as described for nuclear DNA. For each individual, the haplotype designations of each region were combined in sequence creating a composite haplotype.

Molecular data analysis

Nei's (1978) unbiased genetic distance was calculated from the allozyme data by using the computer program BIOSYS2 (Swofford and Selander, 1989). Mean nucleotide

Table 3

PCR primers and conditions used in the RFLP analysis of mtDNA and nuclear intron regions. The forward primer is on top, the reverse is on the bottom.

Region	Primer sequence	PCR conditions	Citation	Enzymes
12S/16S	12SA-L: 5′ AAA CTG GGA TTA GAT ACC CCA CTA T 3′ 16SA-H: 5′ ATG TTT TTG ATA AAC AGG CG 3′	94°C for 1 min., 45°C for 1 min., 65°C for 3 min.	Palumbi et al., 1991	*Ban* II, *Rsa* I
ATPase 6	H8969: 5′ GGG GNC GRA TRA ANA GRC T 3′ L8331: 5′ TAA GCR NYA GCC TTT TAA G 3′	95°C for 1 min., 45°C for 1min., 65°C for 3 min.	Quattro[1]	*Dde* I
ND4	ARG-BL: 5′ CAA GAC CCT TGA TTT CGG CTC A 3′ LEU: 5′ CCA GAG TTT CAG GCT CCT AAG ACC A 3′	95°C for 1 min., 45°C for 1 min., 65°C for 3 min.	Bielawski and Gold, 1996	*Bst*O I, *Hpa* II, *Mbo* I, *Rsa* I
S7 ribosomal	S7RPEX2F: 5′ AGC GCC AAA ATA GTG AAG CC 3′ S7RPEX2R: 5′ GCC TTC AGG TCA GAG TTC AT 3′	95°C for 30 sec., 60°C for 1 min., 72°C for 2 min.	Chow and Hazama, 1998	*Alu* I, *Dra* I
Actin intron	F3: 5′ ATG CCT CTG GTC GTA CCA CTG G 3′ R1: 5′ CAG GTC CTTACG GAT GTC G 3′	94°C for 1 min., 48°C for 1 min., 65°C for 3 min.	Cordes, 2000	*Hinf* I

[1] Quattro, J 1999. Personal commun. Department of Biology, Univ. South Carolina, Columbia, SC 29208.

sequence divergence was calculated for the mitochondrial DNA RFLP results by using the equation of Nei and Li (1979) for fragment data with weighting based on Nei and Tajima (1983) as performed by the computer program REAP (McElroy et al., 1992). Genetic distance was not calculated for the nuclear DNA loci owing to an absence of shared restriction fragments between *C. fulva* and *P. furcifer*.

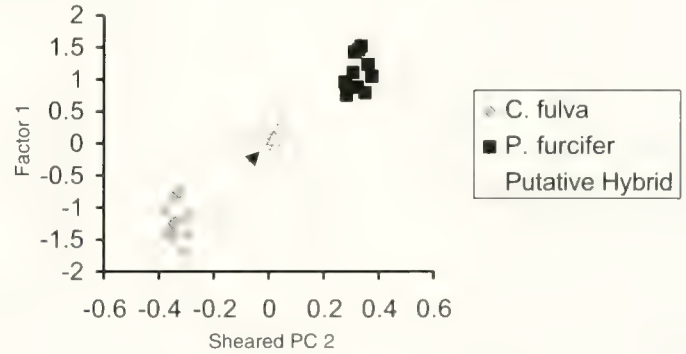

Figure 2

Graph of principal component 2 for the morphological data and factor 1 for the meristic data for ten *Cephalopholis fulva*, ten *Paranthias furcifer*, and ten putative hybrids. The arrow indicates putative hybrid H7, an individual identified as a backcross to *C. fulva*, according to the genetic data.

Results

Morphological analysis

Of 44 counts and measurements analyzed, mean values of 38 were different between *C. fulva* and *P. furcifer*, and the putative hybrids were intermediate in morphology to presumed parents for 33 of these characters (Table 4). The mean value for the putative hybrids exceeded the values of either presumed parent species for four characters (caudal peduncle scales, interorbital width, anal base length, and pectoral length) and was lower than either presumed parent species for two characters (orbit length and depressed dorsal length). In the principal component analysis, the first component accounted for 66% of the variation in the data and the second accounted for 23%. Suborbital width, caudal peduncle length, caudal peduncle to upper fin rays and caudal penduncle to lower fin rays were the characters with the highest loadings. In the meristic data, the first principal component accounted for 62% of the variation. Dorsal rays, gill rakers, and transverse scale rows had the highest loadings. A plot of the second principal component from the morphological analysis (variation in shape) and the first factor of the correlation matrix of the meristic data shows a discrete difference between the putative parents (Fig. 2). Hybrid individuals were shown to be intermediate between the putative parent species.

Allozyme analysis

Sixteen allozyme loci were surveyed in 15 *C. fulva* and 15 *P. furcifer* to identify those that had different alleles in

Table 4

Ranges of counts and measurements for ten *Paranthias furcifer*, ten *Cephalopholis fulva*, and ten putative hybrids. Measurements are given in millimeters. Raw measurements were divided by the standard length and multiplied by 1000. Means are given in parentheses, L.L. = lateral line, and the measurement for one hybrid discarded because of a broken third dorsal spine (*).

Measurement	*C. fulva*	Putative hybrids	*P. furcifer*
dorsal rays	IX, 15–16 (16)	IX, 17–18 (17)	IX, 18–19 (19)
anal soft rays	8–10 (9)	9–10 (9)	9–11 (10)
pectoral rays	32–35 (34)	35–37 (36)	36–39 (38)
gill rakers	22–28 (25)	24–35 (31)	32–39 (36)
scales above the L.L.	6–8 (8)	10–12 (11)	10–14 (12)
scales below the L.L.	22–27 (25)	26–30 (28)	26–32 (30)
transverse scale rows	64–84 (71)	75–91 (84)	85–96 (91)
caudal peduncle scales	40–49 (46)	44–52 (47)	43–48 (46)
head length	374–427 (402)	320–353 (335)	259–301 (280)
head width	173–227 (200)	150–189 (164)	130–162 (142)
head depth	248–288 (266)	212–250 (233)	183–241 (212)
snout length	86–122 (107)	79–111 (94)	53–79 (67)
suborbital width	44–52 (47)	29–35 (32)	20–24 (22)
interorbital width	64–78 (71)	73–89 (82)	76–89 (80)
orbit length (diameter)	62–76 (68)	56–67 (62)	52–89 (65)
postorbital head length	217–243 (232)	173–210 (192)	146–171 (159)
maxillary length	166–194 (182)	120–163 (141)	96–115 (104)
lower jaw length	176–200 (186)	117–149 (138)	98–114 (105)
snout to angle of preopercle	257–306 (282)	213–246 (229)	176–200 (188)
maxillary width	42–56 (48)	30–45 (41)	28–38 (34)
tip of lower jaw to gular notch	119–181 (145)	90–174 (123)	69–121 (89)
body width	154–223 (178)	155–181 (165)	138–162 (150)
body depth	325–385 (357)	302–361 (332)	282–354 (316)
caudal peduncle depth	128–139 (134)	118–145 (129)	102–122 (111)
tip of snout to dorsal origin	386–422 (407)	334–373 (354)	321–361 (329)
tip of snout to pectoral base	287–415 (371)	293–340 (319)	265–293 (277)
tip of lower jaw to pelvic base	398–449 (420)	359–420 (382)	321–384 (351)
dorsal base length	523–549 (538)	532–561 (543)	543–613 (583)
depressed dorsal length	609–663 (629)	574–643 (609)	603–658 (635)
anal base length	166–187 (174)	171–192 (182)	165–204 (180)
depressed anal length	268–320 (294)	248–273 (261)	232–278 (253)
end of dorsal to caudal base	129–150 (141)	148–165 (157)	145–175 (162)
length of caudal peduncle	166–198 (178)	194–217 (203)	174–241 (219)
pectoral length	257–292 (274)	253–295 (279)	249–290 (274)
pelvic length	186–211 (197)	143–192 (180)	150–187 (173)
dorsal spine I length	54–66 (62)	43–70 (61)	40–64 (53)
dorsal spine III length	103–138 (123)	90–119 (106)	86–117 (105)
dorsal spine IX length	97–150 (127)	104–123 (111)	76–105 (94)
anal spine I length	52–72 (62)	35–66 (53)	36–48 (43)
anal spine II length	95–121 (106)	91–112 (101)	78–98 (86)
anal spine III length	78–118 (108)	97–121 (106)	74–101 (87)
caudal base to tip of upper rays	197–246 (216)	228–304 (280)	321–373 (347)
caudal base to tip of middle rays	204–248 (222)	164–192 (175)	122–143 (128)
caudal base to tip of lower rays	197–242 (217)	278–318 (294)	308–346 (322)

the two species (Table 2). At four loci (*CK-B**, *FH**, *LDH-B**, and *ICDH-S**) *C. fulva* and *P. furcifer* had different alleles. Forty *C. fulva*, 28 *P. furcifer*, one *C. cruentata*, and ten putative hybrids were subsequently screened at the four diagnostic allozyme loci (Table 5). Eight of ten putative hybrids were heterozygous at all four diagnostic loci. One putative hybrid was heterozygous at all loci except the *LDH-B** locus, for which it displayed two alleles characteristic of *P. furcifer*, and another individual was heterozygous at all diagnostic loci, except the *FH** locus

Table 5

Allozyme genotypes of *Cephalopholis fulva*, *Paranthias furcifer*, *C. cruentata*, and putative hybrid individuals at four diagnostic loci, *CK-B**, *FH**, *ICDH-S**, and *LDH-B**. *n* = number of fish in a sample.

	n	*CK-B**	*FH**	*ICDH-S**	*LDH-B**
C. fulva	40	*100/100	†90/90	†95/95	*100/100
P. furcifer	28	†50/50	*100/100	†100/100	*75/75
C. cruentata	1	*100/100	*90/90	*105/105	*75/75
Putative hybrids	8	*50/100	*90/100	*100/95	*75/100
	1	*50/100	*90/100	*100/95	*75/75
	1	*50/100	*90/90	*100/95	*75/100

Table 6

RFLP genotypes for the nuclear intron and mtDNA loci. Some bands (†) were inferred so that fragments would sum to the total (uncut) size of the amplified gene region.

Locus	Enzyme	Allele	Approximate size (bp)
actin intron	*Hinf* I	A	400, 50†
		B	450
S7 intron	*Dra* I	A	575, 550, 75†
		D	1200
		E	575, 525, 75†, 25†
ATPase 6	*Dde* I	A	600, 50†
		B	360, 150, 90, 50†
		C	650
12S/16S	*Rsa* I	A	600, 500, 300, 200
		B	600, 300, 250, 250, 200
		C	450, 375, 300, 275, 100, 100†
	Ban II	A	1600
		B	1100, 500
ND4	*Bst*O I	A	1250, 625, 25†
		B	1250, 450, 200
		C	1450, 450
	Hpa II	A	1400, 500
		C	1900
		D	1000, 900
	Mbo I	A	700, 500, 400, 300
		B	550, 500, 400, 300, 150
		C	525, 400, 300, 275, 250, 80, 70
	Rsa I	A	1025, 500, 375
		B	610, 500, 400, 390
		C	500, 400, 350, 300, 300, 50†
		D	900, 425, 325, 250

for which it displayed two alleles diagnostic of *C. fulva*. *Cephalopholis cruentata* was distinguished from *C. fulva* and *P. furcifer* at the *ICDH-S** locus and was eliminated as a potential parent species.

Table 7

Genotypes of *Cephalopholis fulva*, *Paranthias furcifer*, *C. cruentata*, and putative hybrids for the short actin intron and the second intron in the S7 ribosomal protein region. *n* = number of fish in a sample.

	Actin intron		S7 intron	
Species	*n*	*Hinf* I	*n*	*Dra* I
Cephalopholis fulva	57	A/A	50	A/A
			3	E/E
			4	A/E
Paranthias furcifer	37	B/B	37	D/D
C. cruentata	5	B/B	5	D/D
Putative hybrid	15	A/B	14	A/D
			1	E/D

Nuclear intron regions

An actin intron approximately 450 base pairs in length was amplified. The region was surveyed with 14 restriction enzymes, of which *Hinf* I showed a genetic difference between species. After digestion with *Hinf* I, all *C. fulva* demonstrated allele A, and all *P. furcifer* diplayed allele B (Tables 6 and 7). All fifteen putative hybrids were heterozygous for both alleles.

The second intron region of the S7 ribosomal protein, which was approximately 1200 base pairs in length, was screened with thirty-five enzymes. Two enzymes, *Dra* I and *Alu* I, demonstrated differences between *P. furcifer* and *C. fulva*. *Paranthias furcifer* and *C. cruentata* both exhibited allele D after digestion with *Dra* I (Tables 6 and 7). *Cephalopholis fulva* was variable at this locus—fifty individuals were homozygous for allele A, three homozygous for allele E, and four heterozygous for alleles A and E. All fifteen putative hybrids were heterozygous at this locus with one of the *C. fulva* alleles (A or E), and the *P. furcifer* allele (D). Digestion of the second intron in the S7 region by *Alu* I produced a large number of small fragments that were not easily interpreted and the data were not used

to identify hybridization between *C. fulva* and *P. furcifer*. With this enzyme, however, *C. cruentata* had a unique allele and was thus eliminated as a putative parent for the hybrid individuals.

Mitochondrial DNA

Allelic differences between *C. fulva* and *P. furcifer* were found in all three mitochondrial gene regions. The ATPase 6 region was screened with six enzymes, one of which, *Dde* I, showed differences between *C. fulva*, *P. furcifer*, and *C. cruentata* (Tables 3 and 6). The 12S/16S region was screened with seven enzymes. Two of these, *Ban* II and *Rsa* I, demonstrated differences between *C. fulva*, *P. furcifer*, and *C. cruentata*. The ND4 region was screened with nine restriction enzymes, four of which (*Bst*O I, *Hpa* II, *Mbo* I, and *Rsa* I) showed differences between the species; mtDNA composite haplotypes were unique to each species (Table 8). All 15 putative hybrids in the study had a composite haplotype matching the common haplotype of *C. fulva*, indicating that it was the maternal parent for all hybrid individuals. Three *Epinephelus guttatus* specimens were screened at the ND4 and ATPase 6 regions and showed a unique composite haplotype; therefore this species was not included in the study as a putative parent species.

Discussion

Morphological analysis

In most cases, F_1 hybrids should be morphologically intermediate to the parent species and have low variation within characters among themselves. Backcross individuals, because of random sorting of chromosomes, should have higher variation within intermediate characters and could fall anywhere in the morphological range of the pure parent species (Anderson, 1949). In a principal component analysis plot, a backcross hybrid's score would be expected to be closer to the parent species to which the hybrid backcrossed, whereas an F_1 hybrid's characters would be expected to be in the center, closer to an average of the scores of the parent species.

A plot of the second principal component of the morphological analysis and the first factor of the meristic analysis (Fig. 2) shows that *C. fulva* and *P. furcifer* are well segregated according to morphological characters. The putative hybrid individuals were clustered in between the parent species. The post-F_1 hybrid detected by using genetic analyses, indicated by an arrow in Figure 2, clustered with the putative F_1 hybrid individuals.

Table 8

Composite haplotypes of *Cephalopholis fulva*, *Paranthias furcifer*, and *C. cruentata* for the mitochondrial DNA data. Haplotypes are given for the following sequences of mtDNA loci and enzymes: 1) ATPase 6—*Dde* I, 2) ND4—*Bst*O I, *Hpa* II, *Mbo* I, *Rsa* I; and 3) 12S/16S—*Rsa* I, *Ban* II. *n* = number of fish in a sample.

Species	*n*	Composite haplotype
Cephalopholis fulva	56	AAABBAA
	1	AAABCAA
Paranthias furcifer	36	BBCADBB
	1	BBDADBB
C. cruentata	5	CCDCACB
Putative hybrids	15	AAABBAA

Genetic analyses

Results of the allozyme analysis also supported hybridization between *C. fulva* and *P. furcifer* in Bermuda. The putative hybrids were heterozygous at four distinguishing loci, with the exception of two individuals that were homozygous at one diagnostic locus each. One individual was homozygous at the *LDH-B** locus for the **75* allele. All twenty-eight *P. furcifer* were homozygous for this same allele, indicating hybrid backcrossing to *P. furcifer*. Another hybrid individual was homozygous at the *FH** locus for the **90* allele. The 40 *C. fulva* sampled in this study were homozygous for this allele, suggesting hybrid backcrossing to *C. fulva*. This hybrid individual was among those included in the morphological study and, as shown in the principal component plot (Fig. 2), was morphologically the most similar to *C. fulva*. It was not possible to distinguish F_2 hybrids and backcross hybrid individuals and henceforth the two individuals described above are referred to as post-F_1 hybrids. Because all members of the presumed parent samples were homozygous at all loci for diagnostic alleles, there was no evidence of introgression between *C. fulva* and *P. furcifer*.

The nuclear intron data were consistent with the allozyme data and supported the hypothesis of hybridization between *C. fulva* and *P. furcifer*. Because all hybrid individuals were heterozygous, post-F_1 hybridization was not evident at these loci. Alleles present at both nuclear DNA loci were unique between parent species and there was no indication of introgression between these species.

The mtDNA data clearly showed that *C. fulva* was the maternal parent for all putative hybrids, including the two post-F_1 hybrids. This finding suggests a strong gender bias in hybridization. All *C. fulva* had composite haplotypes quite distinct from those of *P. furcifer*, and there was no evidence of mtDNA introgression between the two parent species.

Overall, the genetic and morphological analyses suggest that all but two of the 15 putative hybrids were F_1 individuals representing first generation hybridization between a female *C. fulva* and a male *P. furcifer* (Table 9). The occurrence of two post-F_1 hybrids indicates that F_1 hybrids are fertile, and the genotypes of the two post-F_1 hybrids demonstrate that F_1 hybrids can backcross with either parent species.

Hybridization in Bermuda

Hybridization between *C. fulva* and *P. furcifer* is known from only certain localities in the tropical Atlantic, despite

Table 9

Classification of all putative hybrid individuals as F_1 and post-F_1 individuals based on morphological and genetic data.

Sample ID	Classification	Data
H1	post-F_1	allozyme, mtDNA, nDNA
H2	F_1	mtDNA, nDNA
H3	F_1	mtDNA, nDNA
H4	F_1	mtDNA, nDNA
H5	F_1	mtDNA, nDNA
H6	F_1	mtDNA, nDNA
H7	post-F_1	morphology, allozyme, mtDNA, nDNA
H8	F_1	morphology, allozyme, mtDNA, nDNA
H9	F_1	morphology, allozyme, mtDNA, nDNA
H10	F_1	morphology, allozyme, mtDNA, nDNA
H11	F_1	morphology, allozyme, mtDNA, nDNA
H12	F_1	morphology, allozyme, mtDNA, nDNA
H13	F_1	morphology, allozyme, mtDNA, nDNA
H14	F_1	morphology, allozyme, mtDNA, nDNA
H15	F_1	morphology, allozyme, mtDNA, nDNA
USNM 124001	F_1	morphology

broad overlap in the geographical ranges of the two species. Bermuda exists at the northern range of *C. fulva* and *P. furcifer*, and the two species have restricted spawning times. *Cephalopholis fulva* and *P. furcifer* both spawn in Bermuda from May to early August (Smith, 1958, as cited in Thompson and Munro, 1978), and spawning individuals of the two species have been sampled in the same location (Burnett-Herkes, 1975; B. Luckhurst, personal observ.). Similarly, two hybrids have been reported from Jamaica where the parent species also have overlapping spawning times (Thompson and Munro, 1978).

Hybridization between *C. fulva* and *P. furcifer* could be the result of directed interspecific interactions, or the chance meeting of gametes spawned at the same time in the same general location. However, because all 13 F_1 hybrids were the result of *C. fulva* eggs fertilized with *P. furcifer* sperm, it appears that there is a gender bias in hybridization. Possible hybridization scenarios include differences in sex ratio between *C. fulva* and *P. furcifer*, a biochemical block on fertilization of *P. furcifer* eggs by *C. fulva* sperm, or "sneaker" *P. furcifer* males in *C. fulva* spawning groups.

Based on the number of individuals collected in Bermuda over the last two years, hybridization between *C. fulva* and *P. furcifer* seems to be relatively rare. Although the reproductive status of the hybrids is unknown, the occurrence of two fertile female F_1 hybrids (one of which was ripe), a spent male F_1 hybrid, and the presence of post-F_1 hybrids, it can be concluded that some F_1 hybrids are capable of producing viable offspring. However, reproduction of F_1 hybrids does not appear to be very extensive. Within the limits of the samples analyzed there was no evidence of introgression of alleles between parent species.

Intergeneric hybridization

Intergeneric hybridization in animals seems to be relatively rare. It is believed that the ability to hybridize is an indication of evolutionary relatedness and that divergent taxa should have lost the ability to interbreed through the evolution of reproductive isolating barriers (Sibley, 1957). However, there are several examples of intergeneric hybridization in fishes, most notably in the cyprinids (Hubbs, 1955; Smith, 1973; Aspinwall et al., 1993; Stauffer et al., 1997).

Intergeneric hybridization between two such ecologically different species as *C. fulva* and *P. furcifer* has also been noted in the lutjanids. Poey (1860) described an intergeneric hybrid between *Lutjanus synagris* and *Ocyurus chrysurus*. Both Loftus (1992) and Domeier and Clarke (1992) presented reviews of this case of hybridization and Loftus (1992) theorized that the species were capable of interbreeding on the basis of overlap of spawning time and habitat. Both Loftus (1992) and Domeier and Clarke (1992) surmised that *O. chrysurus* should not constitute its own genus but be included within the genus *Lutjanus*, owing to its ability to hybridize with a member of that genus. Further support for this revision was provided by Chow and Walsh (1992), who reported a high genetic similarity between *O. chrysurus* and several *Lutjanus* species of the western North Atlantic. They suggested that the species appeared to be misplaced due to its unique morphological features.

A parallel situation exists with the epinepheline serrands because the genetic distance data suggest that *P. furcifer* does not belong in a separate genus from *Cephalopholis*. Recently, Craig et al. (2001) used mitochondrial DNA sequencing to demonstrate a close phylogenetic relationship

between the genera *Paranthias* and *Cephalopholis*. They also cited several morphological and ontogenetic similarities between the two genera. In the present study, an analysis of 16 allozyme loci produced a Nei's (1978) unbiased genetic distance of 0.356 between *P. furcifer* and *C. fulva*, which is within the range reported between *Ocyurus chrysurus* and species of *Lutjanus* (Chow and Walsh, 1992). The mitochondrial DNA sequence divergence data indicated that *P. furcifer* is closer to, or at least no farther from, *C. fulva* (0.036) than is *C. cruentata* (0.042) and that the congeners are most distant, (0.052). Both values are within the range reported between other congeneric serranids (Graves et al., 1990).

Taxonomic revision of *P. furcifer* is not recommended at this time; however, the incidence of hybridization and the small genetic distance between *C. fulva* and *P. furcifer* suggest that a full-scale phylogenetic analysis of the subfamily is warranted. Such a study would have to include more species of *Cephalopholis*, other members of the subfamily Epinephelinae, and *P. colonus*, the eastern Pacific geminate species of *P. furcifer*.

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Effects of experimental harvest on red sea urchins (*Strongylocentrotus franciscanus*) in northern Washington

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Abstract—Commercial harvest of red sea urchins began in Washington state in 1971. Harvests peaked in the late 1980s and have since declined substantially in Washington and other areas of the U.S. west coast. We studied effects of experimental harvest on red sea urchins in San Juan Channel (SJC), a marine reserve in northern Washington. We recorded changes in density and size distribution of sea urchin populations resulting from three levels of experimental harvest: 1) annual size-selective harvest (simulating current commercial urchin harvest regulations), 2) monthly complete (non–size-selective) harvest, and 3) no harvest (control) sites. We also examined recolonization rates of harvested sites. The red sea urchin population in SJC is composed of an accumulation of large, old individuals. Juvenile urchins represent less than 1% of the population. Lower and upper size limits for commercial harvest protect 5% and 45% of the population, respectively. Complete harvest reduced sea urchin densities by 95%. Annual size-selective harvest significantly decreased sea urchin densities by 67% in the first year and by 47% in the second year. Two years of size-selective harvest significantly altered the size distribution of urchins, decreasing the density of legal-size urchins. Recolonization of harvested sites varied seasonally and occurred primarily through immigration of adults. Selective harvest sites were recolonized to 51% and 38% of original densities, respectively, six months after the first and second annual harvests. Yields declined substantially in the second year of size-selective harvest because of the fishing down of the population and because of low recolonization rates of harvested sites. We recommend that managers consider the potential efficacy of marine harvest refuges and reevaluate the existing upper and lower size limits for commercial harvest to improve long-term management of the sea urchin fishery in Washington.

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Red sea urchins (*Strongylocentrotus franciscanus*) are the most commonly harvested species of sea urchin on the west coast of North America. Sea urchin harvest in this region occurs primarily in California, Washington, and British Columbia. The commercial sea urchin fishery in Washington began in 1971, and landings were low through the early 1980s (Fig. 1). Landings increased dramatically in the late 1980s, peaking at over 4000 metric tons (t) in 1988. Landings have since declined. Approximately 387 t of sea urchins were harvested in 2000, valued at $699,052 (Ulrich[1]). Red sea urchins currently constitute approximately 60% of landings—the remainder being green sea urchins (*S. droebachiensis*, Ulrich[1]).

The Washington sea urchin fishery currently is managed by using harvest quotas, size limits, license restrictions, limited entry, and mandatory log books (Lai and Bradbury, 1998). Season length is not limited, but harvest occurs primarily during the winter when roe quality is highest (Bradbury[2]). A rotational harvest strategy was practiced from 1977 until 1995, in which each harvest district (Fig. 2) was harvested once every third year. In 1995 a U.S. federal court ruling on shellfishery management in Washington's coastal marine waters (Shellfish Subproceedings of United States vs. State of Washington, 873 F. suppl. 1422, 1994, known commonly as the "Rafeedie Decision") allotted one half of all harvestable shellfish to native tribes. As a result, rotational harvest was discontinued and replaced by annual harvest to ensure that all tribes had equal access to their usual and accustomed fishing areas each year.

Sea urchin harvests declined substantially in the early 1990s along parts of the west coast (Fig. 1). Quotas and season lengths were reduced in Washington because of overharvesting concerns (Bradbury[2]). Quotas were not reduced in California, and catches declined substantially (Kalvass and Hendrix, 1997). Sea urchin densities in some harvested areas in northern California are less than one quarter of those in nearby reserve areas (Kalvass and Hendrix, 1997). In Washington, densities and the proportion of legal-size sea urchins in the population have declined (Pfister and Bradbury, 1996). Harvesters may be maintaining catch per unit of effort at high levels by exploiting new populations, thereby masking stock declines (Pfister and Bradbury, 1996).

Experimental harvests may indicate potential effects of commercial harvest

[1] Ulrich, M. 2001. Personal commun. Washington State Department of Fish and Wildlife, 600 Capitol Way North, Olympia, WA 98501.

[2] Bradbury, A. 2000. Personal commun. Washington State Department of Fish and Wildlife, Point Whitney Shellfish Laboratory, 1000 Point Whitney Road, Brinnon, WA 98320.

Table 1

Depth and area of study sites in San Juan Channel, Washington. Site numbers are those shown in Figure 2. Initial sea urchin densities are from sampling in permanently marked circular sampling areas in early March 1997.

Site	Abbreviation	Treatment	Depth (m)	Area (m^2)	Initial sea urchin density (no./m^2)
1. Mid San Juan Island	Mid SJI	complete harvest	6.6	428	1.15
2. South McConnell Island	South McConnell	complete harvest	10.4	405	1.13
3. O'Neal Island	O'Neal	complete harvest	5.8	430	1.36
4. Point Caution, San Juan Island	Point Caution	selective harvest	7.5	422	1.95
5. Upper San Juan Island	Upper SJI	selective harvest	9.1	421	1.27
6. North McConnell Island	North McConnell	selective harvest	9.1	415	0.37
7. Yellow Island	Yellow	control	6.9	404	2.05
8. Point George, Shaw Island	Point George	control	7.5	406	1.96
9. Shady Cove, San Juan Island	Shady Cove	control	10.2	447	0.94

on sea urchin populations in Washington. We examined changes in density and size distribution of red sea urchin populations resulting from two levels of experimental harvest. Our study site was San Juan Channel (SJC), one of two areas in Washington where commercial sea urchin harvest has been prohibited since the 1970s (Fig. 2). We compared density and size distribution data for sea urchins from experimentally harvested sites in SJC with similar data collected from 1) nearby control sites, and 2) 19 sites in the Strait of Juan de Fuca (SJDF), an area commercially harvested since the early 1970s. We also examined recolonization of harvested sites through recruitment and immigration. We discuss implications of our results for management of sea urchin harvest effort and the potential use of marine harvest refuges in enhancing Washington's sea urchin fishery.

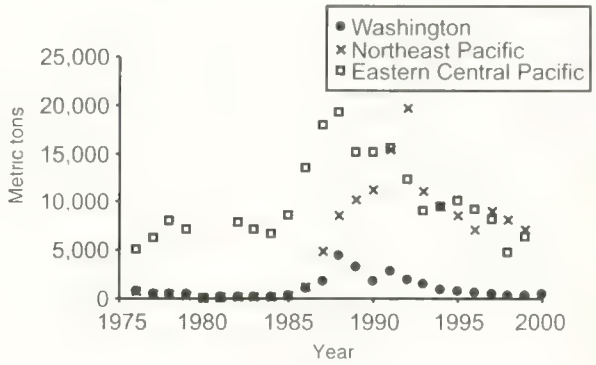

Figure 1

Annual harvest of red sea urchins (*Strongylocentrotus* spp.) in Washington state and in the larger Northeast Pacific and eastern Central Pacific areas of the west coast of the United States. Northeast Pacific includes the area north of 40°30′N (approximately Oregon-California border). Eastern Central Pacific includes the area south of 40°30′N. (Sources: Hoines, 1994, 1998; FAO, 1980, 1981, 1992, 2001; Bradbury.[2])

Methods

We established nine study sites in SJC from November 1996 to March 1997 (Fig. 2). Sites were 6–10 m in depth and approximately 10 m × 40 m, with the long axis of each site running parallel to the shoreline along the depth contour (Table 1). Eight permanently marked circular sampling areas (each 7.07 m^2) were located along the midline of each site along the depth contour. Site selection was based on high red sea urchin density (≥1.5/m^2 in preliminary surveys), substrate (primarily large cobble or bedrock) and safety considerations.

We applied one of three harvest treatments to each site. "Selective harvest" consisted of annual removal of all legal-size sea urchins (102–140 mm test diameter) each winter (March of 1997 and 1998). Selective harvest simulated the annual commercial harvest of a bed of sea urchins in the San Juan Islands (Pfister and Bradbury, 1996). "Complete harvest" consisted of removal of all sea urchins present in March 1997, and at monthly intervals thereafter through September 1998. The complete harvest treatment did not represent any current management strategy for commercial harvest. Rather, the complete harvest treatment represented one extreme (the control treatment being the second) against which effects of selective harvest may be compared. Sea urchin densities were not manipulated in the "control" treatment. Because of logistical constraints, control sites were located in smaller preserve areas within SJC where harvest of all invertebrates and fish is prohibited. Harvest treatments were randomly assigned to the remaining six sites. All sea urchins harvested were measured at the surface and released at other locations in SJC well away from the study sites.

In SJC, we sampled at large (sites) and small (circular areas within sites) spatial scales. Small-scale sampling was more frequent, allowing detection of potential short-

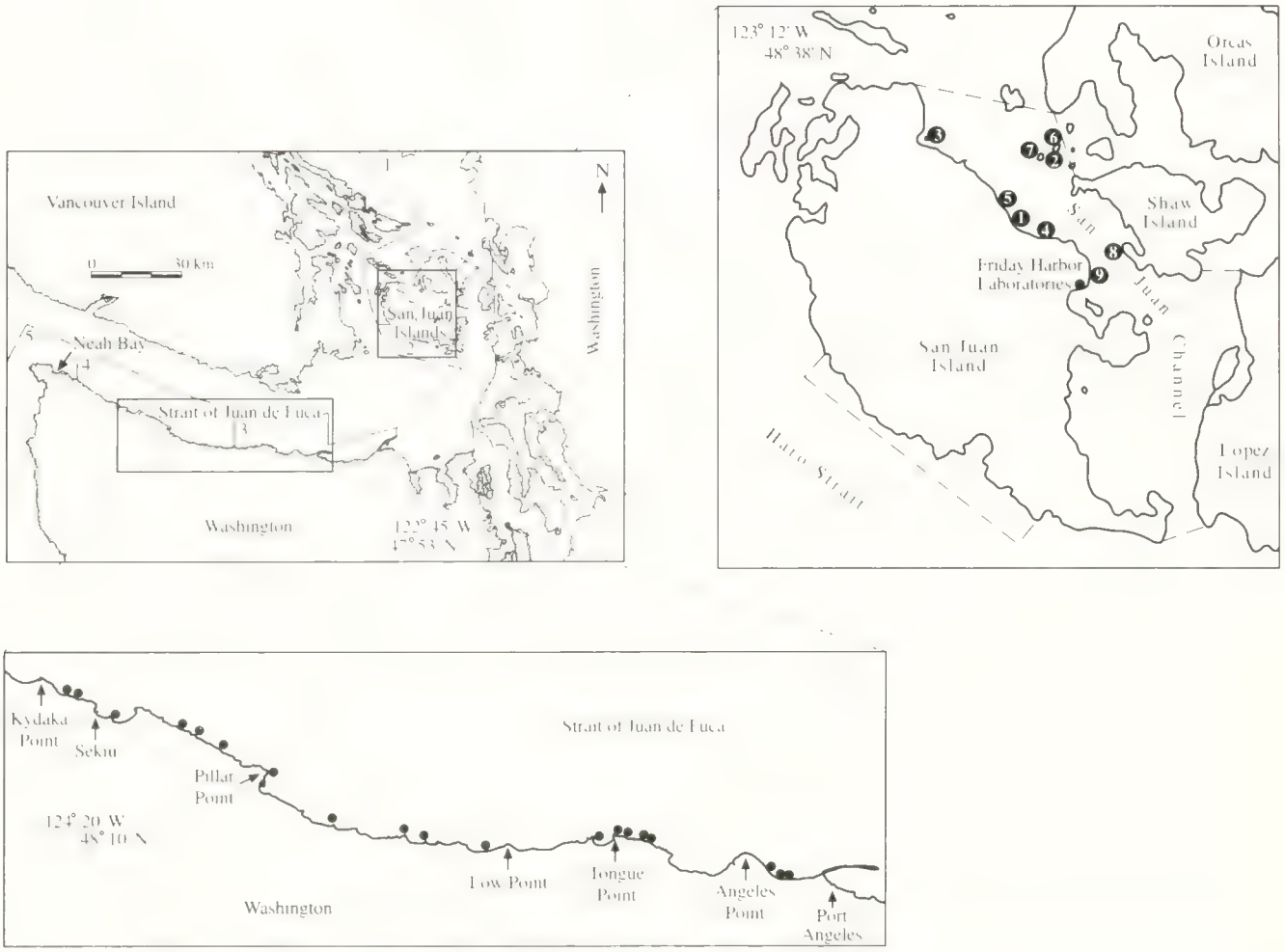

Figure 2

(**Upper left**) The commercial harvesting districts for sea urchins in Washington (after Lai and Bradbury, 1998). Harvest district numbers are shown in the upper left corner of each district. (**Right**) Enlargement of San Juan Channel, showing locations of study sites. Sites 1–3 are complete harvest sites, sites 4–6 are selective harvest sites, and sites 7–9 are control sites. Dashed lines represent the boundary of the areas on the west coast of San Juan Island and in San Juan Channel closed to commercial sea urchin harvest through fall 1998. The dotted line represents the modified southern boundary of the reserve area in San Juan Channel established in fall 1998. (**Lower left**) Enlargement of the Strait of Juan de Fuca sampling area. Black circles indicate locations of randomly chosen sampling sites.

term effects of harvest; whereas large-scale sampling better indicated how treatments affected the entire bed of sea urchins. We identify the scale of sampling (sites vs. circular areas within sites) for all results.

Size distribution

In SJC, we measured all sea urchins removed during the initial harvest of complete and selective harvest sites in March 1997, and all sea urchins removed during the second annual harvest of selective harvest sites in March 1998. In September of 1997 and 1998, we measured a minimum of 100 sea urchins *in situ* in all sites in randomly chosen 5 m × 5 m quadrats. We also measured sea urchins in the circular areas within sampling sites *in situ* in all sites five times per year: early March, mid March, April, June, and September. The sampling periods represented preharvest and 5, 30, 90, and 180 days after harvesting in each year for the selective harvest treatment.

Nineteen randomly chosen sites in the western SJDF were sampled in August and September 1997 (Fig. 2). All sites were 7–8 m below mean lower low water. At each site, we measured sea urchins *in situ* on 1–3 transects parallel to shore, each ≥30 m^2.

Lower and upper size limits for commercial sea urchin harvest are 102 and 140 mm test diameter in SJC, and 83 and 114 mm in SJDF (Pfister and Bradbury, 1996). Sea urchin measurements in SJC and SJDF were recorded to the nearest 5 mm (e.g. 130 mm=test diameters 130–134 mm), except during the initial sampling periods (March–June 1997), when sea urchins measured *in situ* only were recorded to the nearest 10 mm (e.g. 130 mm=test diameters

130–139 mm). Because of the measurement increment used, we could only estimate proportions of under-, legal-, and over-size sea urchins in SJC and SJDF. Asterisks (*) indicate estimated size classes. Estimated size classes are as follows: SJC—under*-size: 0–95 mm, legal*-size: 100–135 mm, and over*-size: 140–175 mm; SJDF—under*-size: 0–80 mm, legal*-size: 85–110 mm, and over*-size: 115–175 mm. Sea urchins less than 50 mm are less than two years old and were classified as juveniles (see Pfister and Bradbury, 1996).

Harvest and recolonization

Recolonization was determined for three periods: summer 1997 (March 1997 [postharvest]–September 1997), winter 1997 (September 1997–March 1998 [preharvest]), and summer 1998 (March 1998 [postharvest]–September 1998). In complete harvest sites, monthly recolonization for each time period was calculated as the sum of the number of sea urchins removed each month from each site during the time period divided by the number of months in the time period. A few sea urchins that divers did not harvest in March 1997 because they could not safely be removed from the substrate were excluded from the calculation of recolonization for the first time period. Size of recolonizers was based on sea urchins harvested from May 1997 to September 1998. In selective harvest sites where sea urchins were removed only once each year, we calculated monthly recolonization for each time period as the difference between the number of sea urchins counted in each site at the beginning and end of the time period, divided by the number of months in the time period.

At the end of the study (September 1998), divers sampled destructively for juvenile sea urchins in one 0.80-m^2 wedge within each circular area within a sampling site. Prior to this time, divers may not have seen very small sea urchins concealed underneath rocks or large sea urchins because sampling was not destructive to avoid disturbing other experiments. We include results on both red and green juvenile sea urchins sampled because of the very low number of red sea urchins sampled and to provide an indication of the microhabitats inhabited by juvenile sea urchins in general in SJC.

Data analysis

Size-frequency data were grouped into discrete size classes and compared by using chi-square analysis. Sea urchin data collected at each site were correlated over time. Therefore, we used a paired t-test to analyze the effect of harvest on the total number of sea urchins in sites and on the density of sea urchins in each size class. Similarly, we analyzed sea urchin densities in permanent circular areas over time by using repeated measures analysis of variance. In the analysis, site was treated as a random factor and was nested within treatment, which was treated as a fixed factor. Densities of juvenile sea urchins in September 1998 were analyzed by using analysis of variance. Sea urchin densities were log-transformed to improve the variance structure for analysis (Zar, 1984). Mean values generally are followed by one standard deviation in the text. The level of significance for all tests was $\alpha = 0.05$.

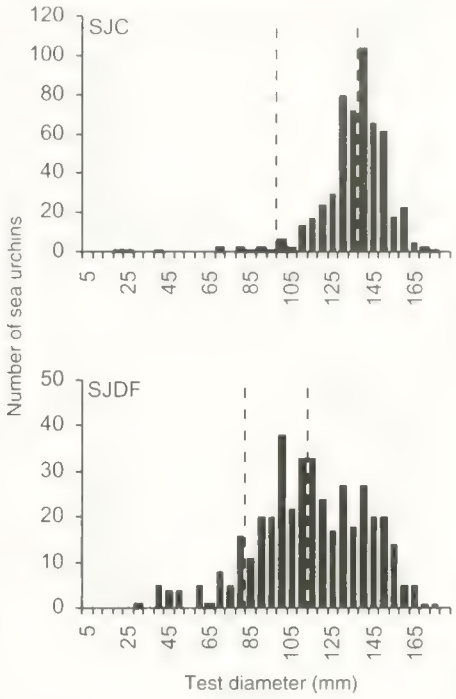

Figure 3

Size-frequency distribution of red sea urchins sampled in the three control sites combined in San Juan Channel (SJC) in September 1997 (n=537) and in the western Strait of Juan de Fuca (SJDF) in August 1997 (n=405). Dashed lines indicate minimum and maximum size limits for commercial harvest in each location.

Results

Size distribution of sea urchins in SJC and SJDF

Size distributions of red sea urchins in SJC were strongly skewed to the right and had a modal size of 140 mm (range 20–175 mm, Fig. 3). 4.8% (±3.1%) of sea urchins in circular areas in all sites in early March were <100 mm (under*-size), 50.0% (±13.0%) were 100–139 mm (legal*-size), and 45.2% (±12.5%) were ≥140 mm (over*-size). Juveniles represented 0.3% (±0.4%) of the population.

The modal size of red sea urchins in SJDF was 100 mm (range 30–175 mm, Fig. 3). 12.1% of the red sea urchin population was under*-size, 35.6% was legal*-size, and 52.4% was over*-size. Juveniles represented 2.5% of the population.

Effect of harvest on size distribution

Sea urchins harvested in the initial size-selective harvest in 1997 were 90–160 mm in diameter (mode 135 mm,

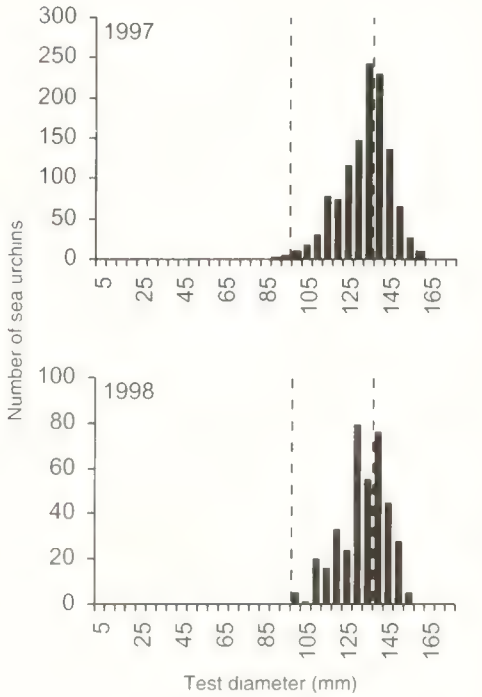

Figure 4

Size distribution of red sea urchins harvested from the three selective harvest sites combined in San Juan Channel (SJC) in March 1997 (n=1194) and March 1998 (n=387). Dashed lines indicate minimum and maximum size limits for commercial harvest in SJC.

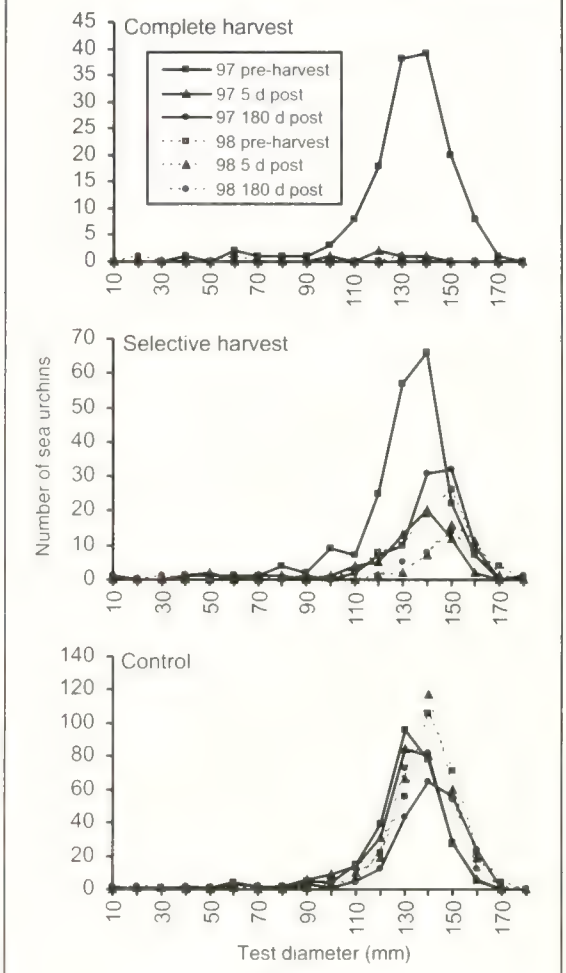

Figure 5

Size distribution of red sea urchins in the complete harvest, selective harvest, and control treatments in San Juan Channel (SJC) in early March (before harvest), mid-March (five days after harvest), and September (180 days after harvest) of 1997 and 1998. Solid lines represent sampling periods in 1997, and dashed lines represent sampling periods in 1998. Cumulative sample sizes for the three sites within each treatment and for all sampling periods illustrated are n = 149, 518, and 1627 for the complete harvest, selective harvest, and control treatments, respectively. Samples are from urchins measured *in situ* in sampling circles. One site (mid SJI) was excluded from the 1997 early March sampling period for the complete harvest treatment.

Fig. 4). The harvest consisted of 0.5% (±0.4%) under*-size sea urchins, 59.5% (±6.6%) legal*-size sea urchins, and 39.9% (±9.2%) over*-size sea urchins. Sea urchins harvested in the second annual size-selective harvest in 1998 were 100–155 mm in diameter (mode 130 mm). The composition of the harvest was similar: 0.0% (±0.0%), 57.1% (±18.7%), and 42.9% (±18.7%) of sea urchins were under*-, legal*-, and over*-size, respectively.

The initial size-selective harvest did not significantly alter the size distribution of the population (P=0.18, Fig. 5) but did significantly reduce the density of legal*-size sea urchins (P=0.05, Table 2). The cumulative effect of two annual size-selective harvests on the size distribution of the population was highly significant (P<0.0001, Fig. 5) and significantly reduced the density of legal*-size sea urchins (P=0.03, Table 2). The modal size of sea urchins in selective harvest sites increased to 150 mm after the second annual harvest (Fig. 5). Six months after the second annual harvest, the size distribution of the population remained significantly different from the original (1997 preharvest) size distribution (P=0.0001). Size distributions of sea urchins in selective harvest sites did not differ between fall 1997 and fall 1998 according to large-scale sampling (P=0.06), averaging 5.8%, 34.3%, and 60.0% for under*-, legal*-, and over*-size sea urchins, respectively (n=756). Size distributions of sea urchins in control sites, based on small-scale sampling, were similar throughout the study (Fig. 5) and did not differ between fall 1997 and fall 1998 according to large-scale sampling (P=0.10).

Table 2

Changes in the density (no./m^2) of under*-, legal*- and over*-size sea urchins as a result of selective harvests in March of 1997 and 1998. Values are averages (±SD) of the three selective harvest sites and are based on sea urchins sampled in permanent circular sampling areas within each site. See text for explanation of size categories.

	1997			1998		
	Preharvest	5 days after harvest	180 days after harvest	Preharvest	5 days after harvest	180 days after harvest
Under*-size	0.06 (±0.06)	0.03 (±0.04)	0.01 (±0.02)	0.00 (±0.00)	0.01 (±0.01)	0.01 (±0.01)
Legal*-size	0.62 (±0.37)	0.14 (±0.10)	0.18 (±0.24)	0.14 (±0.18)	0.04 (±0.06)	0.07 (±0.05)
Over*-size	0.52 (±0.39)	0.20 (±0.13)	0.37 (±0.18)	0.32 (±0.06)	0.19 (±0.08)	0.15 (±0.10)

Table 3

Total number of sea urchins (±SD) in San Juan Channel study sites over time. Harvests occurred in early March of 1997 and 1998. "Postharvest" data were collected immediately after the harvest by divers performing the harvest. SJI = San Juan Island.

	1997			1998		
Site	Preharvest	Postharvest	180 days after harvest	Preharvest	Postharvest	180 days after harvest
Complete harvest						
O'Neal Island	511	19				
Mid SJI	639	40				
South McConnell	641	37				
Average	597 (±74)	32 (±11)				
Selective harvest						
North McConnell	261	100	173	181	113	147
Upper SJI	560	206	229	207	92	139
Point Caution	907	228	421	430	226	290
Average	576 (±323)	178 (±68)	274 (±130)	273 (±137)	144 (±72)	192 (±85)
Control						
Yellow Island			547			646
Point George			823			859
Shady Cove			347			266
Average			572 (±239)			590 (±300)

Effect of harvest on density

Sea urchin densities in the SJC sites initially averaged 1.35/m^2 (±0.55, Table 1). Differences in initial sea urchin density between sites were marginally significant (P=0.05) because of the low density of sea urchins at North McConnell. Because of the difference in initial density, we expressed changes from preharvest to postharvest densities in SJC sites as percentages of the original population.

Initial harvest in March 1997 decreased the number of sea urchins in complete harvest sites by 94.7% (range: 93.7–96.3%) and in selective harvest sites by 66.6% (range: 61.7–74.9%, Table 3). Reharvest of selective harvest sites in March 1998 reduced sea urchin numbers 46.9% (range: 37.6–55.6%). All decreases were significant ($P \leq 0.04$). Yields from selective harvest sites averaged 0.95 sea urchins/m^2 in 1997, and 0.31 sea urchins/m^2 in 1998. The number of sea urchins in control sites did not differ between 1997 and 1998 (P=0.77, average 1.41/m^2).

Small-scale sampling also demonstrated significant changes in sea urchin density as a result of the experimental harvest treatments (Table 4). Initial harvest reduced sea urchin densities by 97.6% and 69.5% in complete and selective harvest sites, respectively. Mid-March (5 days after harvest) densities averaged 0.03/m^2 (±0.07/m^2) and 0.37/m^2 (±0.45/m^2) in complete and selective harvest sites, respectively. Sea urchin densities in complete harvest sites remained low for the duration of the study (<0.04/m^2). Sea urchin densities in selective harvest sites increased slight-

Table 4

Summary of repeated measure analysis of variance results for red sea urchin density. In cases where the degrees of freedom for the tests of significance for the within-subjects effects were adjusted by the Huynh-Feldt epsilon, the unadjusted degrees of freedom are given in parentheses. Asterisks in column five indicate factors significant at the 0.05 level. Power was estimated by using graphs in Zar (1984). (—) indicates that power was very low for the effect but could not be computed exactly (Sokal and Rohlf, 1995).

Source	Degrees of freedom	Mean square	*F*-ratio	*P*-value	Observed power
Within-subjects effects					
Year	1	0.24	1.88	0.22	<0.20
Year × treatment	2	0.11	0.88	0.46	—
Year × site (treatment)	6	0.13			
Season	3.56 (4)	0.28	14.34	* 0.000	>0.99
Season × treatment	7.11 (8)	0.055	2.78	* 0.033	0.44
Season × site (treatment)	21.34 (24)	0.020			
Year × season	3.72 (4)	0.12	9.42	* 0.000	0.98
Year × season × treatment	7.45 (8)	0.070	5.32	* 0.001	0.86
Year × season × site (treatment)	22.34 (24)	0.013			
Between-subjects effects					
Intercept	1	22.11	214.92	0.000	1.00
Treatment	2	6.79	14.99	* 0.005	0.95
Site (treatment)	6	0.45			

Table 5

Monthly recolonization (no. of sea urchins/site) for complete and selective harvest sites from April 1997 through September 1998. The summer and winter time periods are April–September and October–March, respectively. SJI = San Juan Island.

Treatment	Site	Summer 1997	Winter 1997	Summer 1998
Complete harvest	O'Neal Island	22.7	11.7	16.0
	Mid SJI	29.5	13.8	34.2
	South McConnell	16.3	4.7	6.3
	Average	22.8	10.1	18.8
Selective harvest	North McConnell	12.2	1.3	5.7
	Upper SJI	3.8	3.7	7.8
	Point Caution	32.2	1.5	10.7
	Average	16.1	0.3	8.1

ly in the summer following each harvest (see next section). Sea urchin densities in control sites changed little over time, averaging 1.61/m^2 (±1.4/m^2) over the study period.

Recolonization of harvested sites

Recolonization of complete harvest sites averaged 17.2 sea urchins per month (range: 0–68), or 0.04/m^2 month. The average size of sea urchins recolonizing complete harvest sites was 129 mm (±19 mm, range: 35–175 mm, n=824). Recolonization of complete harvest sites was higher during the summer of each year than during the winter and decreased slightly but not significantly over time (P=0.31, Table 5).

Recolonization of selective harvest sites was lower than observed in complete harvest sites (average 7.9 sea urchins/month or 0.02/m^2 month, Table 5). Recolonization was highest during summer 1997, followed by summer 1998. There was no net recolonization during winter 1997. Sites were recolonized to 51.2% of original densities by September 1997 (range: 40.9–66.3%, Table 3). In September 1998, after two annual harvests, sites averaged 37.7% of original densities (range: 24.8–56.3%).

Juvenile recruitment

Juvenile sea urchins were rare in all SJC study sites in March 1997 (0.4% (±0.6%) of sea urchins sampled in

Table 6

Modal size and proportion of juveniles in red sea urchin populations along the west coast of North America.

Location	Modal size (mm)	% of juveniles	Source
Southeast Alaska, shallow habitats	100–120	~35% <60 mm	Carney, 1991
Southeast Alaska, deep habitats	140–160	~8% <60 mm	Carney, 1991
Vancouver Island, BC	100–120	<5% <30 mm, ~50% <100 mm	Watson, 1993
Vancouver Island, BC	100–150*	~7% <50 mm*	Breen et al., 1978
Vancouver Island, BC	80–150*	0–11% <50 mm*	Breen et al., 1976
Strait of Georgia, BC	100–139*	9.5% <50 mm*	Sloan et al., 1987
San Juan Channel, Washington	140–144	0.3% <50 mm, 4.8% < 100 mm	This study
Strait of Juan de Fuca, Washington	100–104	2.5% <50 mm, 24.7% <100 mm	This study
Northern California	~107	~8–12% <50 mm	Rogers-Bennett et al., 1995; Smith et al., 1998
San Nicolas Island, Southern California	100–120	~7% < 50 mm	Cowen, 1983
Southern California	25 and 110	39% < 30 mm	Tegner and Dayton, 1981

* Commercially harvested populations

circular areas). Over the entire study period, juvenile red sea urchin densities in circular areas averaged 0.005/m^2 in control sites (0.6% of the population), 0.001/m^2 in selective harvest sites (0.9% of the population), and 0.0006/m^2 in complete harvest sites. Sampling at the larger spatial scale revealed similar results. Juvenile sea urchin density averaged 0.002/m^2 in control sites in September of both 1997 and 1998. Juvenile sea urchin density averaged 0.001/m^2 and 0.005/m^2 in selective harvest sites in September of 1997 and 1998, respectively.

Invasive sampling in September 1998 confirmed that juvenile sea urchins were rare in SJC sites during the study. One juvenile (13 mm) red sea urchin and 45 juvenile (2–12 mm) green sea urchins were found in a search of 6.4 m^2 of substrate in each site (57.6 m^2 total). Density of juvenile green sea urchins sampled did not differ between treatments (P=0.79; average 0.79/m^2 [±0.86]). Only 4.3% of the juvenile green sea urchins were associated with (found within 8 cm of) an adult red sea urchin. 26.7% of juvenile green sea urchins were found in cryptic microhabitats (algal holdfasts), and the remainder were found on algal blades or on top of cobble, boulders, or bedrock.

Discussion

Size distribution of sea urchins in SJC and SJDF

The modal size of sea urchins in SJC is larger than observed in most other locations on the west coast (Table 6). The size distribution of red sea urchins in SJC sites is strongly skewed toward large individuals. The slow growth rate of sea urchins in Washington (Lai and Bradbury, 1998), combined with the fact that SJC was, at the time of our study, a reserve area that has never been subject to significant harvest, indicates that the sea urchin population in SJC is composed primarily of older individuals. Fewer juveniles are present in SJC and SJDF than in most other areas on the west coast (Table 6). Large recruitment events appear to be rare for red sea urchins in SJC, evidenced by the lack of peaks in the size distribution at small test diameters.

Effect of harvest on size distribution

The first annual size-selective harvest only slightly affected the size distribution of sea urchins in SJC. The cumulative effect of two annual size-selective harvests was significant, however, significantly reducing the density of legal*-size sea urchins in the population and increasing the modal size of the population. Commercial fisheries elsewhere along the west coast have also affected the size distribution of sea urchin populations. Three commercial harvests in the San Juan Islands (outside the SJC reserve) over a nine-year period decreased the proportion of legal-size sea urchins by about 73% (Pfister and Bradbury, 1996). In southern California, two years of harvest reduced the proportion of legal-size sea urchins in shallow waters by 15% (Tegner and Dayton, 1981). In northern California, the modal size of sea urchins in unharvested reserve sites was 108 mm, whereas the modal size of sea urchins in nearby heavily harvested sites with a 76-mm minimum size limit was 73 mm (Smith et al., 1998). On the east coast of Vancouver Island, however, the modal size of sea urchins remained above the legal size limit after 3+ years of significant harvest (Sloan et al., 1987).

The modal size of the sea urchin population and the upper size limit for legal harvest coincided in SJC. Small errors in the measurement of sea urchins by divers led to an incomplete harvest of legal-size sea urchins and inadvertent "poaching" of many over-size sea urchins (41% of the catch, likely a slight overestimate because sea urchins

140 mm in diameter were incorrectly classified as over-size). Both actions would tend to minimize effects of our experimental size-selective harvest. Commercial harvesters take a much smaller proportion of over-size sea urchins (11.2% of catch) and harvest a higher proportion of legal-size sea urchins (Pfister and Bradbury, 1996). Thus commercial harvest should produce larger differences in size distribution than observed in our study.

Effect of harvest on sea urchin density

Commercial harvest in nonreserve habitats of the San Juan Islands for over two decades has significantly decreased sea urchin densities (Pfister and Bradbury, 1996). Both harvest treatments in our study reduced sea urchin densities dramatically and immediately, as expected. The accumulation of older larger individuals in the SJC population led to high yields in selective harvest sites in 1997. Yields in selective harvest sites declined by more than two thirds in 1998 owing to the fishing down of the population (Hilborn and Walters, 1992), low immigration of legal-size sea urchins, and the presence of few under-size sea urchins in the population with a potential of growing to legal size.

Recolonization of harvested sites

Recolonization of harvested sites occurred primarily by immigration of adult red sea urchins. Recolonization began within one month of harvest and continued for the next 18 months. In northern California sites at 11 m in depth, red sea urchins also immigrated into harvested sites within a short time period (Rogers-Bennett et al., 1998). Complete and selective harvest sites in California were recolonized to 32% and 86% of their original densities, respectively, within nine days. These recolonization rates are much higher than those observed in SJC, possibly because of high sea urchin movement (up to 10 m/h, Rogers-Bennett et al., 1995, 1998) and smaller study plots (64 m^2 per site) in the northern California location. Sea urchins move less (~1 m/day) in areas with abundant food, such as in SJC, than in areas with little food (Mattison et al., 1977; Carney, 1991).

Seasonally high recolonization rates observed each spring in both harvest treatments may be related to feeding activity. Spring and summer are seasons when sea urchins feed more frequently (Vadas, 1968) and densities of algae preferred by sea urchins in SJC (e.g. *Laminaria, Nereocystis*, *Alaria*, and *Costaria*; Vadas, 1968, 1977) are highest (Carter, 1999). Both factors may have stimulated movement of sea urchins from deeper waters (with lower algal densities) into our sites.

On a monthly basis, selective harvest sites were recolonized at about half the rate at which complete harvest sites were recolonized. Sea urchins recolonizing complete harvest sites were removed monthly, whereas those recolonizing selective harvest sites were not. The presence of sea urchins, however, did not inhibit immigration in another study (Watson, 1993). Differences in sea urchin densities in adjacent habitats or food availability may have contributed to the observed differences in recolonization rates both within and between treatments.

Recolonization of selective harvest sites was insufficient to maintain sea urchin populations at the densities and size distributions observed prior to harvest under an annual harvest scenario. A site in Washington was recolonized to preharvest density and size distribution after 2.5 years (Bradbury, 1991). Recolonization of SJC sites varied substantially in the first year following harvest (range 1–202 sea urchins per site). One year, after harvest, sites varied between 37% and 69% of their original densities. Such variability in recolonization between sites may be common and should be considered when estimating recolonization rates for commercially harvested areas.

Recolonization rates observed in this study should be considered maximum estimates for recolonization of commercially harvested areas. SJC study sites were small, and sea urchins were relatively abundant adjacent to sites. Commercial fishermen harvest entire beds of sea urchins before moving on to the next bed and prefer to harvest at shallow depths (Pfister and Bradbury, 1996; Kalvass and Hendrix, 1997; Bradbury[2]). Thus sea urchins in adjoining habitats at the same depth would likely be harvested, and only sea urchins inhabiting deeper waters would be available for recolonization.

Juvenile recruitment

The unimodal size distribution of red sea urchins and the rarity of juvenile red sea urchins in SJC suggest variable and infrequent red sea urchin recruitment in northern Washington. In central California, red sea urchin recruitment was also rare; no major recruitment events occurred during a ten-year period (Pearse and Hines, 1987). Size structures of other sea urchin populations north of Point Conception also suggest low red sea urchin recruitment (Table 6).

Commercial harvest may negatively affect juvenile recruitment in several ways. Commercial harvest decreases sea urchin densities in northern Washington (Pfister and Bradbury, 1996; our study), potentially decreasing fertilization rates and larval supply (Levitan et al., 1992). A reduction in adult sea urchin density might also negatively affect juveniles in benthic habitats because adult sea urchins may provide associated juveniles with protection from predators (Duggins, 1981; Breen et al., 1985) and provide an increased food source (Tegner and Dayton, 1977, but see Andrew and Choat, 1985). In southern and northern California, 81% and 73%, respectively, of juvenile red sea urchins were found under the spine canopy of adults (Tegner and Dayton, 1977; Rogers-Bennett et al., 1995). In southern California, juvenile sea urchins were less abundant in harvested sites than in control sites (Tegner and Dayton, 1977). In northern California, juvenile red sea urchins were rare or absent in completely harvested sites but were present in similar numbers in selectively harvested and control sites (Rogers-Bennett et al., 1998). In British Columbia, 69% of juvenile red sea urchins were associated with adults (Breen et al., 1985). Adults may be less important to juveniles in SJC than in other west coast areas because few (4.3%) juvenile green

sea urchins were found to be associated with adult red sea urchins (our study), juvenile abundance did not differ by harvest treatment (our study), refuge habitats (cobble, crevices, kelp holdfasts) are abundant, and fast moving sea urchin predators (e.g. fish, lobster) are rare or absent (Breen et al., 1985; Sloan et al., 1987).

Management implications

The current harvest strategy in Washington, applied to sea urchin beds in SJC, results in low yields in the second year of harvest owing to the fishing down of the population and slow recolonization of harvested areas. Annual commercial harvest of a single location is probably not economically viable. Commercial harvests in Washington and other areas of the west coast are well below levels observed in the late 1980s, and biomass estimates are not available to evaluate the status of stocks in Washington (Bradbury[2]). In such circumstances, options for managing the fishery to conserve, and possibly increase, stocks over the long term include artificially enhancing stocks, redirecting or reducing harvest, and establishing marine harvest refuges (Tegner, 1989; Quinn et al., 1993; Rogers-Bennett et al., 1995). Stock enhancement efforts often confer limited success (e.g. Tegner, 1989) and may negatively impact behavioral and genetic diversity of wild populations (Rogers-Bennett, 1997).

Sea urchin harvest in Washington is currently controlled by using harvest quotas, limited entry, and size limits; seasonal closures and rotational harvests were also employed until relatively recently (Pfister and Bradbury, 1996; Lai and Bradbury, 1998). Washington also has two marine harvest refuges (Fig. 2). Both rotational harvests and marine harvest refuges increase the probability of long-term survivorship of populations, particularly when recruitment is low and variable, as it appears to be in SJC (Botsford et al., 1993; Quinn et al., 1993; Pfister and Bradbury, 1996). Rotational harvests were discontinued in Washington in 1995, and the size of one of the two marine harvest refuges was reduced substantially in 1998 (Fig. 2). Additional marine harvest refuges in Washington might be established in areas difficult for harvesters to access (e.g. areas hazardous to navigation and far from port) with little decrease in the actual size of harvested areas (Starr, 1998). Critical to the effectiveness of marine harvest refuges in enhancing recruitment and fishery yields outside of refuge areas is the ability of larvae produced in refuges to recruit to areas outside of the refuge (Carr and Reed, 1992). The extended period that sea urchin larvae spend in the plankton (9–19 weeks, Strathmann, 1978) and the short residence time of water in SJC (Thomson, 1981; Hickey et al., 1991) suggest that larval dispersal from this and other refuge areas to areas outside of the refuge is highly likely, probably occurring on a scale of tens to hundreds of kilometers. Research on sea urchin recruitment patterns (including larval dispersal, settlement, and juvenile survival) in this region is needed to assess the potential for marine harvest refuges in Washington to contribute to recruitment of fished stocks in Washington.

The current size limits in SJC protect a substantially smaller proportion of the population than in SJDF (50% vs. 63%, respectively). Because there are very few small sea urchins in SJC, the lower size limit protects less than 5% of the population. The upper size limit, established to protect larger "broodstock," currently protects 45% of the population. Size limits in Washington were originally established to protect the lower and upper 20% of the population and to allow some individuals to grow through the legal-size "window" under a three-year rotational harvest policy (Pfister and Bradbury, 1996). Considering the small number of juveniles in the population and the return to an annual harvest in 1995, the existing size limits should be reevaluated for their efficacy at protecting local stocks in the context of other harvest control techniques.

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Age and growth of the smooth dogfish (*Mustelus canis*) in the northwest Atlantic Ocean

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Abstract—The northwest Atlantic population of smooth dogfish (*Mustelus canis*) ranges from Cape Cod, Massachusetts, to South Carolina. Although *M. canis* is seasonally abundant in this region, very little is known about important aspects of its biology, such as growth and reproductive rates. In the early 1990s, commercial fishery landings of smooth dogfish dramatically increased on the east coast of the United States. This study investigated growth rates of the east coast *M. canis* population through analysis of growth patterns in vertebral centra. Marginal increment analysis, estimates of precision, and patterns in seasonal growth supported the use of vertebrae to age these sharks. Growth bands in vertebral samples were used to estimate ages for 894 smooth dogfish. Age-length data were used to determine von Bertalanffy growth parameters for this population: K = 0.292/yr, L_∞ = 123.57 cm, and t_0 = –1.94 years for females, and K = 0.440/yr, L_∞ = 105.17 cm, and t_0 = –1.52 years for males. Males matured at two or three years of age and females matured between four and seven years of age. The oldest age estimate for male and female samples was ten and sixteen years, respectively.

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The smooth dogfish, *Mustelus canis*, is a small shark species found throughout the western Atlantic Ocean from Massachusetts to Florida, and in the northern Gulf of Mexico, including Cuba, Jamaica, Barbados, Bermuda, Bahamas, and southern Brazil to northern Argentina. Smooth dogfish are demersal and typically are found in inshore continental shelf and slope waters (Compagno, 1984). Several discrete populations of smooth dogfish likely exist, separated by large geographic areas; and there appears to be little intermigration between the different populations (Bigelow and Schroeder, 1948). The northwest Atlantic population of smooth dogfish ranges from Cape Cod, Massachusetts, to South Carolina and migrates seasonally in response to changing water temperatures (Bigelow and Schroeder, 1948; Castro, 1983).

Recently, commercial harvest of smooth dogfish has increased on the east coast of the United States. Annual landings were under 80,000 pounds before 1990, over 300,000 pounds in 1990, and increased to around 1 million pounds from 1998 to 2000. In one year (1995) landings exceeded 2.5 million pounds (Fig. 1) (NMFS, 2002). Smooth dogfish have been landed in significant amounts (i.e. over 50 metric tons) in Massachusetts, New Jersey, Maryland, Virginia, and North Carolina (NMFS, 2002).

Sharks are often highly susceptible to overfishing because of life history traits that include slow growth, large adult size, late reproduction, and the production of a few large well-formed young (Hoenig and Gruber, 1990). Because of these characteristics, shark fisheries tend to decline drastically after a short time and take long periods to recover (Holden, 1974). The determination of how increased exploitation will affect a shark population, like that of *M. canis* in the northwest Atlantic Ocean, requires information on the growth and reproductive rates of the species targeted by the fishery. The purpose of this study was to determine the growth rates of smooth dogfish from the northwest Atlantic Ocean by using age estimates derived from vertebral growth-band counts.

Materials and methods

Smooth dogfish were collected from NMFS groundfish and longline surveys, Virginia Institute of Marine Science (VIMS) longline surveys, Grice Marine Laboratory longline surveys, the Massachusetts state trawl survey, and by the Massachusetts Division of Marine Fish-

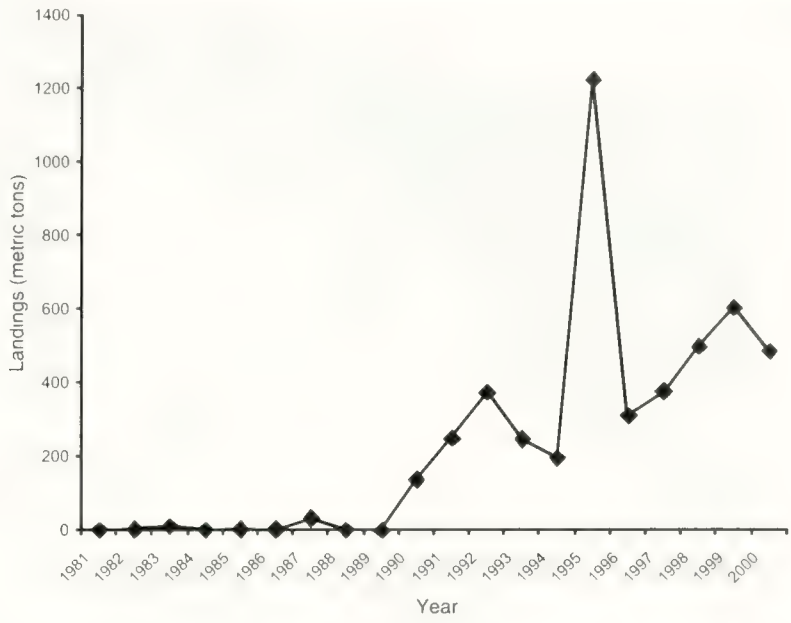

Figure 1

Reported smooth dogfish landings from National Marine Fisheries Service commercial catch statistics for the Atlantic and Gulf states, from 1981 to 2000.

eries (MDMF). Total length (TL), precaudal length (PCL), and male clasper length (CL) were measured, and sex was recorded at the time of collection. A section of the vertebral column containing eight to twelve vertebrae was removed from directly under the first dorsal fin and stored frozen. Reproductive samples were taken from smooth dogfish at this time and maturity state was assessed from these samples.

Vertebral samples were cleaned, soaked in 70% ETOH for 24 hours, and air-dried for 24 hours. Dried vertebrae were sagitally sectioned through the focus with an Isomet rotary diamond saw (Buehler, Lake Bluff, IL). Afterwards, vertebral sections were affixed to microscope slides with mounting medium and polished with wet fine-grit sand paper to a thickness of about 0.5 mm. The vertebrae were viewed under a binocular dissecting microscope with transmitted light.

Vertebral radius was measured from the focus of the vertebra along the axis of the corpus calcarium to the edge of the vertebra (Fig. 2). Total length (TL) was plotted against vertebral radius (VR) to determine if the growth of the vertebra was proportional to somatic growth of the animal and whether the structure was appropriate for estimating growth rate of the animal.

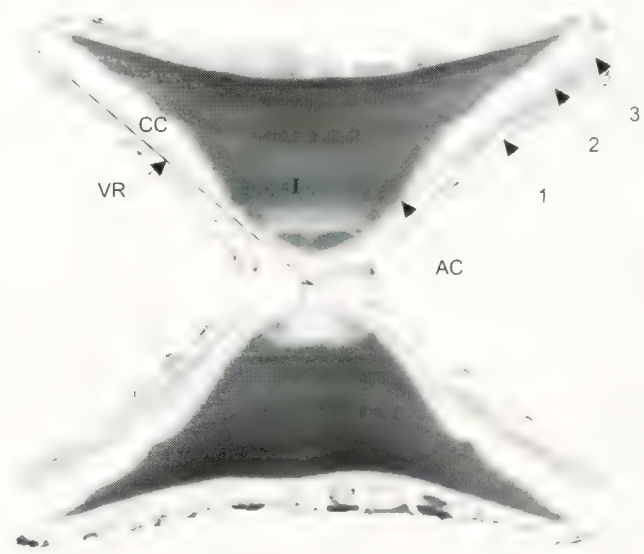

Figure 2

An age-3+ *Mustelus canis* vertebra, VR = vertebral radius, AC = angle change denoting birthmark, 1, 2, 3 = age 1, 2, and 3 growth bands, CC = corpus calcareum, and I = intermedialia.

Growth patterns of the vertebrae consisted of wide translucent bands separated by narrow opaque bands that extended from the intermedialia to the corpus calcareum (Fig. 2). An angle change—the result of a change in growth rates at this time—was present in the intermedialia approximately 2 mm from the focus of each vertebra and was considered to be a birthmark. Age was estimated by enumerating the narrow opaque bands, which were considered to form annually owing to a slowing or stopping of

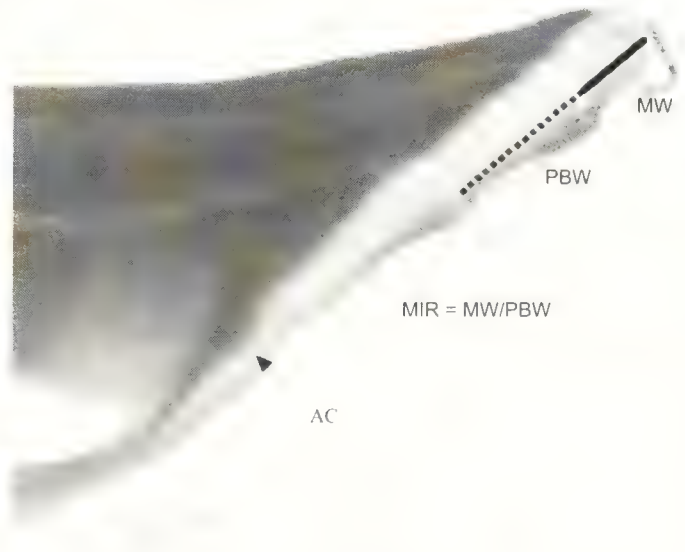

Figure 3

An age-2+ *Mustelus canis* vertebra showing the calculation of the marginal increment ratio, MW = margin width, PBW = previous band width, MIR = marginal increment ratio, AC = angle change.

growth during the winter months. This study followed the criteria found in Casey et al. (1985), who defined an "annulus" as a mark that appears as an opaque band in the intermedialia and continues as an opaque band into the corpus calcareum.

A random sample of twenty vertebrae from each of ten 10-cm size classes (33–132 cm TL) was read independently by two readers, and a chi-square test was used to test for systematic differences between the ages. The number of observations above the main diagonal of a contingency table of reader one's and reader two's ages was compared with the number of observations below the main diagonal to determine if this ratio was significantly different from 1:1. The percent agreement (PA), i.e. the percentage of vertebrae in each length group that were assigned the same ages by both readers, was determined to test for precision between the two readers.

Marginal increment analysis verified the annual nature of the narrow opaque growth bands. The distance from the last opaque band to the edge of the margin was measured and divided by the width of the last growth band on the vertebra to determine the marginal increment ratio (MIR, Fig. 3). The margin width was divided by the distance to the angle change or birthmark for age-1 animals. For age-0 animals, the distance from the angle change to the edge of the vertebrae was measured and divided by the distance from the focus to the angle change. The mean MIR for each month was plotted for juvenile-size animals to determine if there was a yearly pattern in margin width.

The length-at-age data were used to generate a von Bertalanffy growth curve for males and females by using the computer program SigmaPlot (SPSS Inc., 2000) and the Marquardt-Levenberg algorithm to estimate curve-fitting parameters (Press et al., 1986; Marquardt, 1963; Nash, 1979; Shrager, 1970, 1972).

To determine if there was a period of the year when smooth dogfish were growing at a faster rate, the mean total length of age-0 and age-1 smooth dogfish was plotted for each month. For this procedure, we used data from several years and we assumed that every year class followed the same general growth pattern during the first two years of life. The mean monthly length of age-0 animals determined for the 1997 and 1998 cohorts was also calculated. Because we did not collect free-swimming age-0 *M. canis* during May, the largest estimate of birth length (40 cm) was used to minimize the possibility of creating an artificially large growth increment during the summer months.

Results

Vertebrae were collected from 918 smooth dogfish ranging in size from 33 to 132 cm TL. The relationship between TL and VR for males and females was not significantly different (ANCOVA, $P<0.05$); therefore the data for both sexes were combined. The statistically significant relationship ($P<0.001$) between TL and VR was positive and curvilinear (Fig. 4):

$$TL = -0.477(VR)^2 + 17.06\,(VR) + 0.807$$
$$[n=833,\ r^2=0.97,\ P<0.001].$$

Of the original 918 vertebral samples, 894 animals were aged and vertebrae from 24 animals were found to be un-

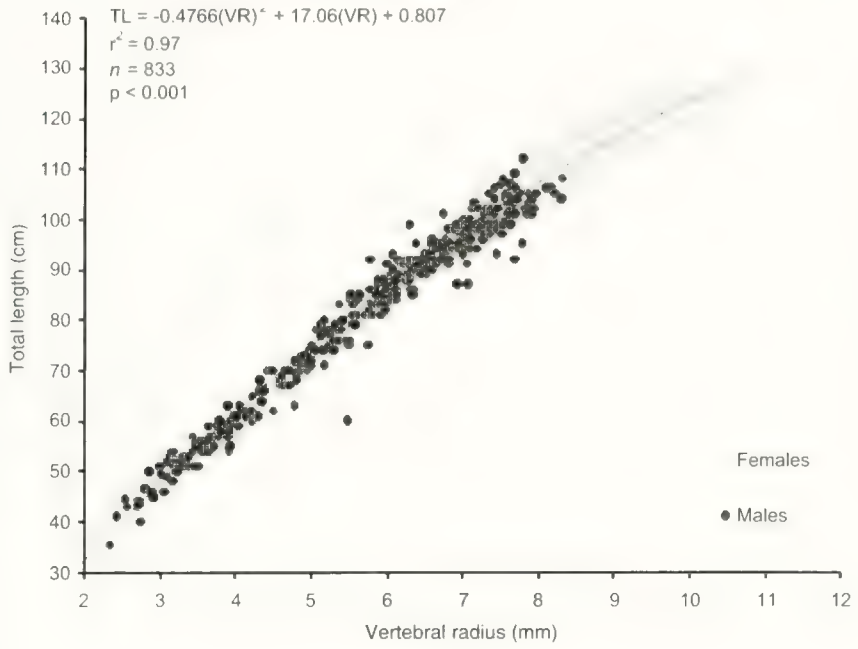

Figure 4

Relationship between vertebral radius (VR) and total length (TL) for *Mustelus canis*.

Table 1

Contingency table of reader one's ages versus reader two's ages, the bold numbers are along the main diagonal (where reader one's age = reader two's age).

		Reader one															
		0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Reader two	0	**53**															
	1		**19**	2													
	2		1	**19**	1												
	3				**19**												
	4				3	**2**	1										
	5					2	**6**	1									
	6						2	**11**	2								
	7								**14**								
	8									**4**							
	9									1	**2**						
	10									1	1	**1**					
	11										1	2	**2**	1			
	12											1	1	**2**			
	13											2	1		**2**		
	14														**0**	1	
	15															**0**	

readable. To test for precision, a second reader read vertebrae from a total of 185 animals (twenty from each 10-cm size group, except for the 33–42 cm size group [n=9]) and four vertebrae were found to be unreadable. A contingency table of reader one's versus reader two's ages was made and a chi-square test resulted in a $\chi^2 = 3.19$, which was less than the critical value of $\chi^2_{0.05,1} = 3.84$; thus the hypothesis of symmetry was not rejected (Table 1). The overall percent

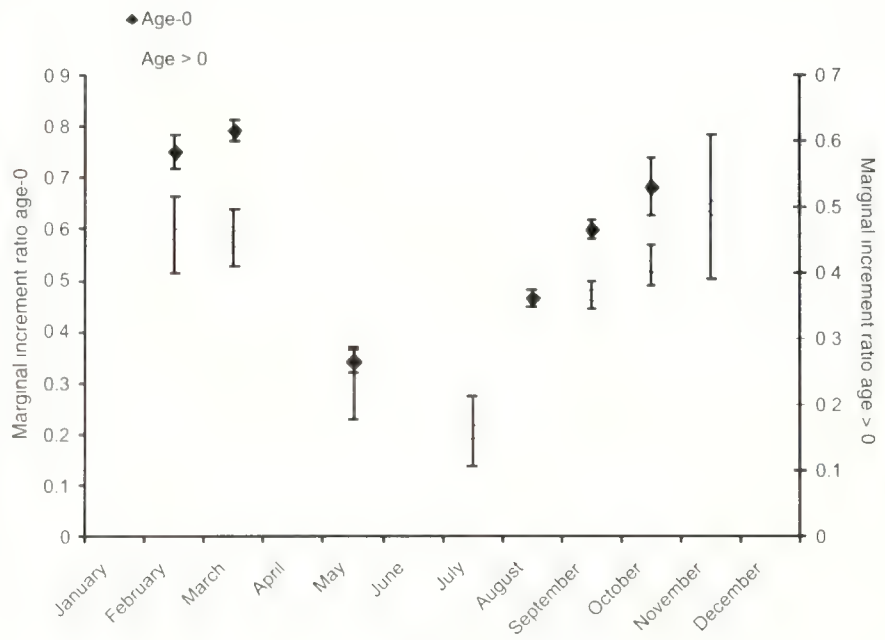

Figure 5

Monthly average marginal increment ratio for male (TL<86 cm) and female (T<102 cm) smooth dogfish (error bars are standard error).

Table 2

Percent agreement (PA) between reader one's ages and reader two's ages for each 10-cm size group.

Size group	Total vertebrae read	No. of vertebrae aged in agreement	No. of vertebrae aged in agreement ±1 year	PA	PA ±1 year
33–42 cm	9	9	9	100	100
43–52 cm	20	20	20	100	100
53–62 cm	20	20	20	100	100
63–72 cm	20	20	20	100	100
73–82 cm	19	16	19	84.21	100
83–92 cm	20	18	20	90	100
93–102 cm	20	15	20	75	100
103–112 cm	19	15	18	78.95	94.74
113–122 cm	19	13	18	68.42	94.74
123–132 cm	19	11	15	57.89	78.95
Total	185	157	179	84.86	96.76

agreement between the two readers was over 84% and the percent agreement within one year was over 96% (Table 2). Agreement within one year was high (over 90%) for all size groups except the largest, where it dropped to 79%.

The largest marginal increments were observed in vertebrae from animals collected in March (Fig. 5). A large drop in marginal width appears to occur in May indicating that band formation most likely occurs during April. The marginal analysis was only conclusive for juvenile-size animals (males less than 86 cm TL, females less than 102 cm TL). By the time these animals become mature, their growth has slowed dramatically and the difference between margin widths becomes very small, making it difficult to elucidate monthly changes in margin width.

Von Bertalanffy growth parameters were calculated separately for males and females because of the approxi-

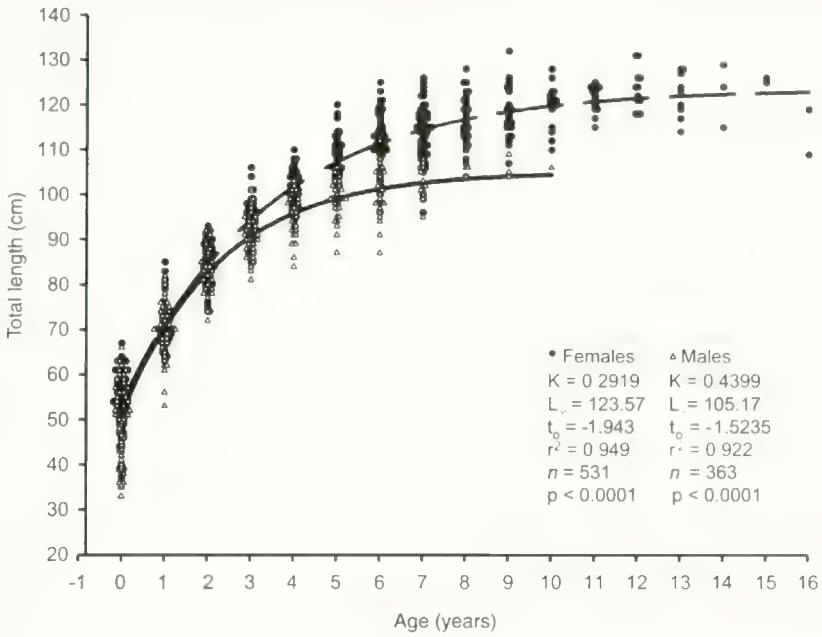

Figure 6

Von Bertalanffy growth function parameters for male and female *Mustelus canis*.

mately 20-cm size difference in both maximum length and length at maturity for males and females. Female growth parameters (Fig. 6) were L_∞ = 123.57 cm, K = 0.2919/yr, and t_0 = −1.9432 years (Table 3). The largest female was 132 cm TL, and 50% of females were found to mature at 102 cm TL and at four to five years of age (Conrath and Musick, 2002). The oldest estimated age for a female smooth dogfish in the study was 16 years and age of the largest female was estimated at nine years old. Male growth parameters (Fig. 6) were L_∞ = 105.17 cm, K = 0.4399/yr, and t_0 = −1.5235 years (Table 3). The largest male in the study was 112 cm TL, and 50% of males were found to mature at 85 cm TL and two to three years of age (Conrath and Musick, 2002). The oldest estimated age for a male smooth dogfish in the study was 10 years, and age of the largest male was estimated at six years old.

The plot of seasonal growth of age-0 and age-1 smooth dogfish indicated a plateau in growth between the months of October and February or March, suggesting slow growth during this period (Fig. 7). There was also a plateau in growth between October and February for both the 1997 and the 1998 cohorts. The mean TL of the 1997 cohort in September 1997 was 51.62 cm (n=31, SE=0.552) and the mean TL of the 1998 cohort in September 1998 was 53.39 cm (n=23, SE=0.579), whereas the mean TL of the 1997 cohort in February 1998 was 57.89 cm (n=18, SE=0.836) and the mean TL of the 1998 cohort in February 1999 was 57.29 cm (n=14, SE=1.605). Assuming a birth length of 40 cm, age-0 animals grew approximately 12–14 cm between May and September and only 4–7 cm between September and February.

Table 3

Von Bertalanffy growth parameters for *Mustelus canis*. SE = standard error.

Parameter	Male	Female
L_∞	105.17	123.56
L_∞ SE	1.0402	0.7353
K	0.4399	0.2919
K SE	0.0226	.0089
t_0	−1.5235	−1.9432
t_0 SE	0.0740	.0641
r^2	0.922	0.949
n	363	531
P	<0.0001	<0.0001

Discussion

Precision estimates, marginal increment analysis, and seasonal growth patterns justify the use of vertebrae as an aging tool for the North Atlantic population of smooth dogfish. The agreement within one year between two readers was high for all size groups (>90%) with the exception of the largest size class (123–132 cm). At this length it becomes very difficult to interpret the margin of the vertebrae and to distinguish between real growth bands and growth checks. Therefore, the maximum age may be

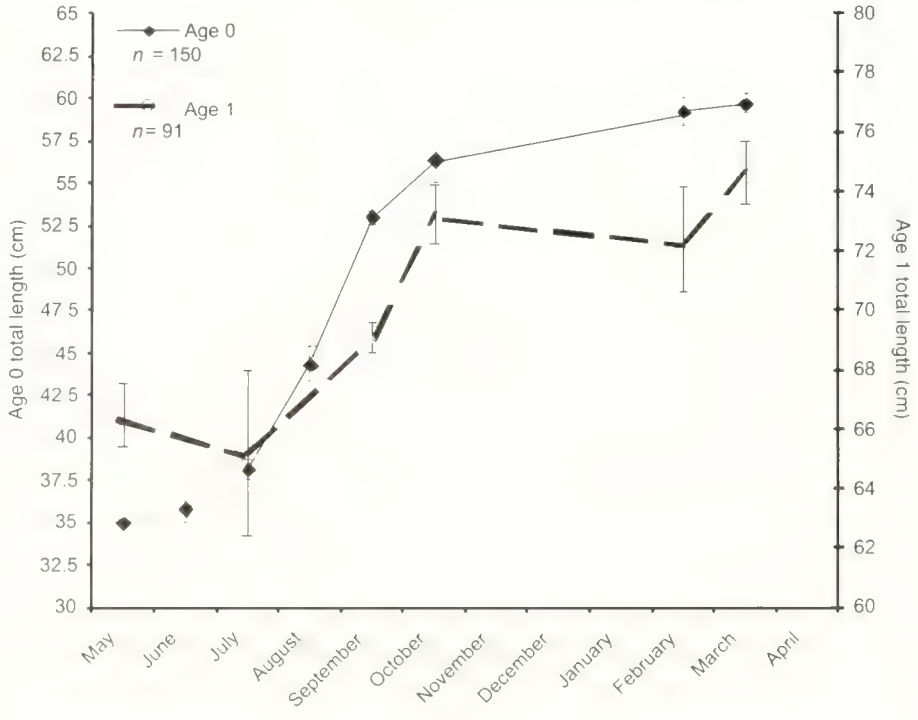

Figure 7

Seasonal growth for smooth dogfish, *M. canis*. Solid line and dashed line show mean size by month of age-0 and age-1 animals (error bars are standard error), respectively.

slightly older or younger than the reported maximum of 16 years for females and 10 years for males.

The marginal increment analysis included only animals of length less than or equal to the length of 50% maturity; therefore the annular nature of the growth bands was verified for these length groups only. Although the marginal widths of the largest animals in the population were too small to discern seasonal differences in these widths, we assumed that these animals follow the same patterns of growth throughout their lifespan.

Estimates of seasonal growth indicated that animals in this population experience a plateau in growth during the winter months between October and February or March, at least for the first two years of life. Their major period of growth is during the summer, between March and October. This finding supports the well established conclusion that an opaque band is deposited annually at the time of slowing or cessation of growth during the winter months. Resuming a faster growth rate after February or March supports the conclusion that a growth band becomes visible in the months of April or May.

Moss (1972) constructed von Bertalanffy growth curves for smooth dogfish by relating tooth width to body length. He estimated that smooth dogfish mature after about one year and reach their maximum size in seven to eight years. He acknowledged that his estimated growth curve did not account for variation in tooth replacement rate and seasonal differences in body growth rate. Francis (1981) estimated von Bertalanffy growth rates by extrapolation from embryonic growth rates using Holden's (1974) method, but this method has subsequently been discredited for application to sharks by Pratt and Casey (1990).

Rountree and Able (1996) used length-frequency analysis to determine growth rates in young of the year (YOY) smooth dogfish in a New Jersey estuary. YOY animals born in May at 29–38 cm TL reached 55–70 cm TL by October of the same year. We found a slightly slower growth rate: age-0 animals in October 1999 ranged from 53–60 cm with a mean size of 56.3 cm (n=6, SE=1.31). We found smooth dogfish grew to a mean of 66.5 cm TL in their first year (size range 61–69 cm, mean size of estimated age-1 May captures, n=13, SE=0.924). The majority of smooth dogfish used in this study were collected in Virginia and North Carolina; therefore geographical differences in growth or differences in growth between years may have contributed to the small discrepancy between our results and those of Rountree and Able.

Values of K reported from various *Mustelus* species (Table 4) ranged from 0.1 for male *Mustelus lenticulatus* from Pegasus Bay, New Zealand, to 0.695 for male *Mustelus manazo*, and from 0.049 for female *Mustelus antarcticus* to 0.42 for female *Mustelus lenticulatus* from Hauraki Gulf, New Zealand (Tanaka and Mizue, 1979; Yudin and Cailliet, 1990; Francis and Francis, 1992; Moulton et al.,

Table 4

Age and growth parameters for *Mustelus* species.

Species	Sex	K	L_∞	t_0	Age at maturity (yr)	Reference
M. californicus	M+F	0.168	154.4	–1.271	1–4	Yudin and Cailliet (1990)
M. henlei	M+F	0.244	97.7	–1.296	1–4	Yudin and Cailliet (1990)
M. manazo	M	0.695	71.4	–0.734	2–3	Tanaka and Mizue (1979)
	F	0.379	88.6	–1.113	2–3	Tanaka and Mizue (1979)
M. manazo	M	0.120	124.1	–2.59		Yamaguchi et al. (1996)
	F	0.113	134.1	–2.55		Yamaguchi et al. (1996)
M. lenticulatus (Pegasus Bay)	M	0.10			5	Francis and Francis (1992)
	F	0.40				
M. lenticulatus (Harakai Gulf)	M	0.16			3.7	Francis and Francis (1992)
	F	0.42			4.7	
M. antarcticus	M	0.160	155.9	–1.94		Moulton et al. (1992)
	F	0.094	233.6	–2.05		
M. mustelus	M	0.12	1451	–2.14	6–9	Goosen and Smale (1997)
	F	0.06	2049	–3.55	12–15	
M. canis	M	0.440	105.17	–1.524	3	Present study, Conrath and Musick (2002)
	F	0.292	123.57	–1.943	4–5	

1992; Yamaguchi et al., 1996; Goosen and Smale, 1997). Smooth dogfish growth coefficients are at the high end of this range (K=0.4399 for males and K=0.2919 for females). Mean asymptotic length of *M. canis* is at the midrange of reported L_∞ values for *Mustelus* species, which range from L_∞ = 71.4, and 88.6 cm for male and female *M. manazo* (Tanaka and Mizue, 1979) to L_∞=155.9 and 233.6 cm for male and female *M. antarcticus* (Moulton et al., 1992). As in nearly all accounts of age and growth for *Mustelis* species, male and female growth in our study was virtually identical in the first few years, and males have a higher growth coefficient (K) than females due to a plateau in growth at a much smaller size (Table 4). However, Francis and Francis (1992) found that female *M. lenticulatus* grow faster than males but still reach a larger maximum length. Their estimates were based on length-frequency data and they acknowledged that the lack of large females may have affected their estimates of von Bertalanffy growth coefficients.

Our growth coefficients for male and female smooth dogfish were comparably high for a shark population; previously reported K values ranged from 0.038 for dusky sharks, *Carcharhinus obscurus* (Natanson et al., 1993) to 1.337 for male Australian sharpnose sharks, *Rhizoprionodon taylori* (Simpfendorfer, 1993). Smooth dogfish grow very quickly for a shark species and mature at a relatively young age. These characteristics may make the northwest Atlantic population more productive and possibly more resilient to exploitation than many other shark populations.

Acknowledgments

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Bycatch of billfishes by the European tuna purse-seine fishery in the Atlantic Ocean

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Abstract—Billfishes are a component of offshore ecosystems; thus it is important to quantify the impact of the tuna fishery on these species in the world's ocean. The aim of this study was to assess the bycatch of billfishes generated by the tropical tuna purse-seine fishery in the eastern Atlantic Ocean. Information on bycatch was collected by observers at sea during the European Union Bigeye Program. With a total of 62 observers' trips, conducted on Spanish and French vessels between June 1997 and May 1999, this project is the biggest observer program ever carried out in the European tuna purse-seine fishery. This study showed that billfish bycatch by the purse seiners is very low (less than 0.021% of the total tuna catches and less than 10% of the total billfish catches currently reported). A Monte Carlo simulation was performed to account for some uncertainties in the fishing strategies of purse seiners operating in this ocean. One of the findings of this study indicated that the temporary moratorium on fishing with FADs (fish aggregating devices), adopted by the European purse-seine fishery in the eastern Atlantic Ocean, produced a decrease in incidental catches of marlins from 600–700 metric tons (t) to less than 300 t. In contrast, this trend was reversed for sailfishes, for which the bycatch increased from 25 t to 45 t. The difficulty of defining indices that express the conservation status in marine fishes and that gauge key ecosystem parameters and the need to promote an ecosystem approach for large-pelagic-resource management which takes into account biologic and socioeconomic criteria are briefly discussed.

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In the spirit of the code of conduct for responsible fisheries it is important to quantify discards and bycatches taken by the main fishing fleets in the world's ocean. Despite recommendations made by different fishery agencies, such as the tuna commissions, this information is rarely reported by skippers in their commercial logbooks. Thus the level of catches of billfishes taken incidentally by the tropical tuna purse-seine fishery is not well-known. In contrast to the recreational fishery, or to some specific small-scale fisheries, billfishes are not targeted by the purse-seine fishery but they can be taken incidentally during the setting operation. In the eastern Atlantic Ocean, parts of bycatch, including billfishes, are kept and are sold in the local African fish market (Romany et al., 2000).

The purpose of this study was to estimate the amount of billfish taken as bycatch by fishing modes (i.e. by FAD [fish aggregating devices] sets, school sets [sets without the use of FADs], and seamount sets) and as bycatch by the Spanish and the French purse seiners in the eastern Atlantic Ocean. Because bycatch information is not recorded in commercial purse seiner logbooks, observations collected by scientific observers aboard purse seiners appeared to be a useful way to assess the amount of bycatch taken by this fleet. Although the European Union Bigeye Program focused on the study of the increase in catch of bigeye tuna (*Thunnus obesus*) by the European tuna-purse seiners in the Atlantic Ocean (Ariz and Gaertner, 1999), information on bycatch was also collected by observers on these purse seiners. We used this data set to estimate the bycatch of billfish in the European purse-seine fishery. These estimates will contribute to the calculation of the total bycatch of billfishes taken in the Atlantic Ocean.

Materials and methods

Data

A total of 62 observer trips (44 for the Spanish fleet and 18 for the French fleet) were conducted opportunistically between June 1997 and May 1999, except from November 1998 through January 1999, a period when there was a moratorium on the use of FADs in fishing operations. In spite of this limitation, this project was the largest observer program ever carried out in the European tuna purse-seine fishery (a total of 2706 fishing days, with 1884 observed sets). The catch of commercial tunas reached 34,693 t, whereas discards (composed mainly of small tuna species or of juveniles of commercial tuna species) were estimated at about 737 t and total bycatch (billfishes,

Table 1

Probabilities of setting with a specific fishing mode k (observed values for a standard year with moratorium and averaged values for a standard year without moratorium; see explanations in the text) and observed conditional probabilities that a specific group of billfish s is associated with this fishing mode. These values were used to perform the Monte Carlo simulation. School sets were made without FADs.

Fishing mode	Number of observed sets	Prob. {fishing mode=k}		Prob. {s present | k}	
		Moratorium	Without moratorium	Marlins	Sailfishes
FAD sets	373	0.2932	0.5500	0.3539	0.0134
School sets	859	0.6753	0.4185	0.0408	0.1036
Seamount sets	40	0.0315	0.0315	0.2500	0.0750

sharks, other fish, etc.) at about 762 t (Ariz and Gaertner, 1999).

Based on the ecological provinces in the oceans established by Longhurst (1998), the eastern tropical Atlantic Ocean (from 25°N to 15°S and from 35°W to the African coasts) was stratified by quarters into two areas:

the Senegalese area (from latitude 12°N to 25°N),
the remaining areas, termed "equatorial" areas.

Owing to time constraints during the set (and bearing in mind that this program was directed at bigeye tuna), it was very difficult for the observer to accomplish some additional bycatch tasks. Consequently, in some circumstances the billfish species may not have been correctly identified. For this reason we established two groups; the blue marlin (*Makaira nigricans*) and the white marlin (*Tetrapterus albidus*) in one group and the sailfishes (*Istiophorus albicans*) and the longbill spearfish (*T. pfluegeri*) in the second group. The weight ranges of billfishes captured as incidental catch by the purse seiners were approximately 130–150 kg for blue marlin, 10–20 kg for sailfish and 45–70 kg for nonidentified marlins (there were no weight estimates for white marlin and longbill spearfish because of their low numbers in the bycatch).

On the basis of a study made on tuna size classes by set type in this fishery (Pallares and Petit, 1998), the sets made on whales and on whale sharks (*Rhiniodon typus*) were classified as school sets (i.e. sets made without FADs) and as FAD sets, respectively. In contrast, it must be stressed that seamounts constitute a specific environment for small size classes of tuna species. In the Atlantic Ocean 2000–3000 t of tunas can be taken yearly on some seamounts (Fonteneau, 1991). Because large pelagic species can be concentrated on seamounts (e.g. sphyrnids, Klimley et al., 1988), we distinguished the sets made on seamounts from the usual tuna fishing modes (i.e. school sets and FAD sets).

Methods

For the two groups of billfishes (i.e. sailfishes and marlins) the total bycatch taken by the European tuna purse-seine fishery in the eastern Atlantic Ocean was estimated for a period of 12 months. The period between October 1997 and September 1998 was considered the best representative standard year for the observer program because it included the best coverage in terms of tuna catches (approximately 17% of the total tuna catch is taken by the European purse seiners from October 1997 to September 1998). Assuming that billfish bycatch was proportional to the tuna catch, the observed bycatch for each billfish group was raised to the total European purse-seine catch with the use of a raising factor RF_{sijk} as in the following equation:

$$TBC_s = \sum_k \sum_j \sum_i RF_{sijk} BC_{sijk},$$

where TBC_s = total bycatch for the group s during a standard year;
RF_{sijk} = total purse seine tuna catch_{ijk}/observed aboard purse seine tuna catch_{ijk};
BC_{sijk} = bycatch for the group s, in area i, quarter j, and fishing mode k;
and $i = 1, 2; j = 1, 2, 3, 4; k$ = school set, FAD set, set on seamount.

Sources of uncertainty in the calculation of the billfish bycatch are caused by 1) changes in fishing strategies adopted by the fishermen over the year, e.g. the probability of choosing the fishing mode k and 2) some features of the bycatch species, e.g. the conditional probability for a given group of billfish s to be present in a set of type k, as well as the probability of obtaining x tons of group s in the set (Table 1). To account for some of these uncertainties our approach differed from that of Perkins and Edwards (1996), who used a modified negative binomial distribution to model bycatch per set. We used computer-intensive methods, such as a Monte Carlo simulation, to estimate the total bycatch generated by the European tuna purse-seine fishery. Monte Carlo methods of simulation introduce a large number of random inputs into a model while recording the range of outputs (Gaertner et al., 1996; Shelton et al., 1997).

In the present analysis, the model mimics the fishing operations made by the purse seiners over a standard

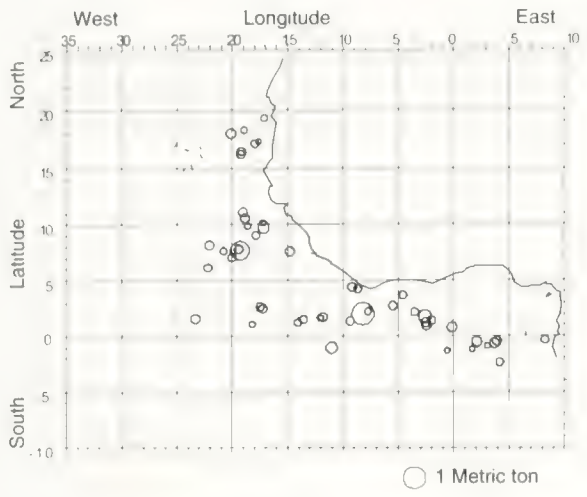

Figure 1

Spatial distribution of the bycatch (t) per school set for the marlin group from the observers' trips during the European Union bigeye tuna program.

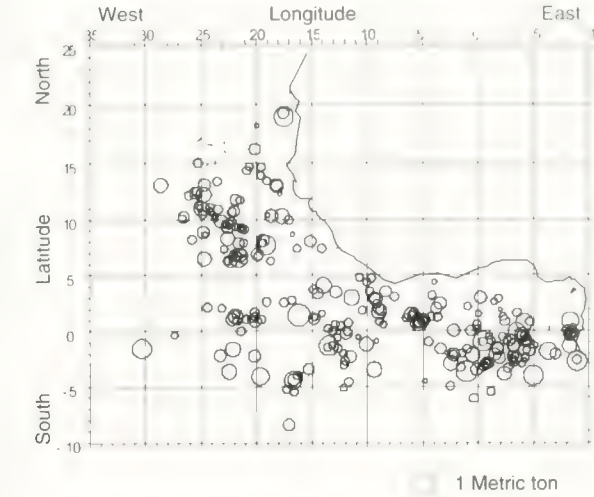

Figure 2

Spatial distribution of the bycatch (t) per FAD set for the marlin group from the observers' trips during the European Union bigeye tuna program.

year. That means that we take into account the probability of setting on the fishing mode k, and the conditional probability that group s is present in this type of set. For each group s, the simulated input (i.e. the bycatch generated by one set) is drawn from the observed distribution of the bycatch by set for the fishing mode k. Note that the calculation of the total bycatch is based on the proportion of total sets (including those made on trips without observers at sea) recorded in commercial logbooks in each strata by fishing mode. That means that the observed bycatch in each set was previously raised by the corresponding raising factor: RF_{ijk}. A single set is then generated by randomly selecting inputs from the distributions of bycatch per set. This is repeated 1272 times (the total number of sets reported by observers aboard) to give the total bycatch of group s during the standard year. 500 Monte Carlo simulations were generated to determine the amount of variation expected in the yearly bycatch estimates. Confidence limits for total bycatch by group were performed by the percentile method.

However, the results obtained in our study may have been affected by the moratorium on fishing with FADs adopted by the French and the Spanish tuna purse-seine companies in the eastern Atlantic Ocean. This temporary ban was adopted over a large area from the African coast to 20°W and from 5°N to 4°S, between 1 November and 31 January in 1997–98 and in 1998–99, respectively. With this consideration in mind, the Monte Carlo simulation was performed a second time to simulate a standard year without a moratorium. We assumed that the probability of setting on FADs (estimated at 0.293 during a year with a moratorium) increases to 0.55 during the years without a moratorium (estimated from commercial logbooks). Consequently, the second Monte Carlo simulation was conducted with the following probabilities: 0.55 (for FAD sets), 0.419 (school sets) and 0.031 (for seamount sets, assuming that the percentage of sets made on seamounts was not affected by a ban on fishing on logs, Table 1).

Table 2

Estimated bycatches of billfishes (t) and observed commercial tuna catches (t) taken by fishing modes by the European purse seiners in the eastern Atlantic Ocean for a standard year (October 1997–September 1998). School sets were made without FADs.

Fishing mode	Marlins	Sailfish	Tuna catches
FAD sets	200.8	7.6	49,214
School sets	42.8	34.7	88,456
Seamount sets	1.5	0.1	1,285
Total	245.1	42.4	138,955

Results

Table 2 shows the estimated bycatch of billfishes taken by each fishing mode during a standard year. The results indicate that 245 t marlin and 42 t sailfishes were taken as bycatch by the European purse seiners in the eastern Atlantic Ocean. Figures 1 and 2 depict the spatial distribution by fishing modes of the marlin bycatch in the eastern Atlantic for all data collected during the observer program. Figure 2 shows that marlin bycatch in FAD sets were spread across a large area in the eastern Atlantic Ocean. When compared to FAD sets, the occurrence of marlins bycatch in school sets was lower, specifically in central

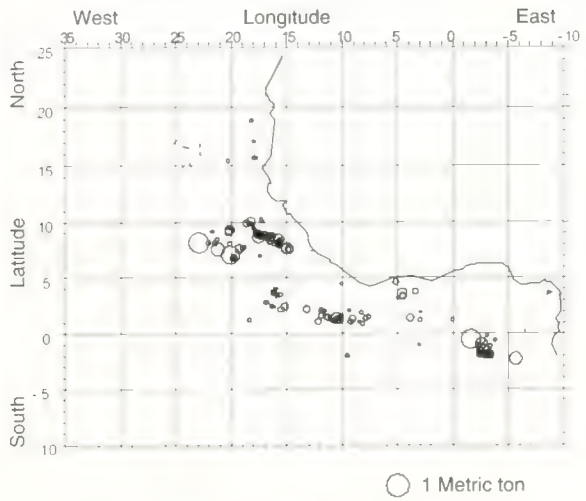

Figure 3

Spatial distribution of the bycatch (t) per school set for the sailfish group from the observers' trips during the European Union bigeye tuna program.

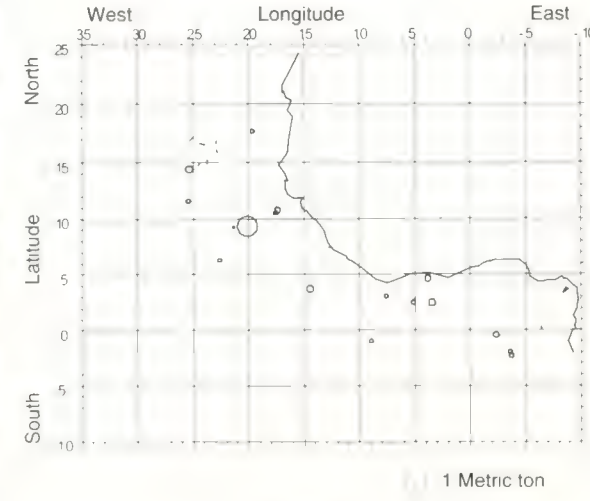

Figure 4

Spatial distribution of the bycatch (t) per FAD set for the sailfish group from the observers' trips during the European Union bigeye tuna program.

Table 3

Results of the Monte Carlo simulation for a standard year with and without a moratorium on FAD sets. Monte Carlo estimates are the average bycatch (t) taken by the European purse seiners in the eastern Atlantic Ocean and the confidence intervals (CI, in tons). "The ratio of billfish to tuna" is the ratio of billfish bycatch to tuna catch (in tons), and corresponding confidence intervals.

	Marlins		Sailfishes	
Group case	Moratorium	Without moratatorium	Moratorium	Without moratorium
Monte Carlo estimates (t)	238.79	396.38	37.52	14.86
Lower CI 0.025	192.86	338.25	23.22	2.89
Upper CI 0.975	283.51	450.54	53.91	33.38
Ratio of billfish to tuna	1.718E-03	2.853E-03	2.700E-04	1.069E-04
Lower CI 0.025	1.388E-03	2.434E-03	1.671E-04	2.076E-05
Upper CI 0.975	2.040E-03	3.242E-03	3.879E-04	2.402E-04

tropical areas. If we compare the spatial distribution of the sailfishes with the spatial distribution of the marlin, we find that the bycatch of sailfishes was associated more with school sets than with FAD sets (Figs. 3 and 4). However, the "sampling scheme" adopted for assessing these incidental catches was constrained by the purse seiners' fishing-effort distribution. Consequently, because purse seiners move seasonally from one area to another, there is a lack of information about the presence of billfishes when the fishing area is temporarily abandoned.

In both runs of the Monte Carlo simulation we used the same conditional probability about the presence of each billfish group by fishing mode (Table 1), as well as for the observed distribution of the bycatch per set by fishing mode. Results indicated that the bycatch of marlins decreased during the moratorium from 396 t to 289 t (Table 3 and Fig. 5). This result is a consequence of the larger association of marlins with floating objects than with school sets. In looking at Table 1, we can see that the occurrence of marlin was around 35% for FAD fishing operations compared to only 4% for school sets. Marlin were also present in 25% of the seamount sets but, from the small number of sets made on seamounts, we could not determined any apparent effect on the total bycatch for this group. Sailfishes were more commonly observed in school sets than in FAD sets (Table 1). Thus it appeared that the bycatch of sailfish increased from about 15 t to 38 t with a moratorium on FADs, as summarized in Table 3 and Figure 5.

Table 4

Estimates of the total bycatch (t) taken by the entire purse-seine fishery in the eastern Atlantic Ocean based on the results of the Monte Carlo simulation applied to the European purse seiners. Because of the moratorium on FAD sets, a decrease of the percentage of FAD sets was assumed for the last three years.

		Marlins			Sailfishes		
Year	Total tuna catch (t)	Estimated bycatch (t)	Lower CI 0.025	Upper CI 0.975	Estimated bycatch (t)	Lower CI 0.025	Upper CI 0.975
1990	211,882	604.50	515.72	686.92	22.65	4.40	50.89
1991	246,110	702.15	599.03	797.89	26.31	5.11	59.12
1992	204,040	582.13	496.63	661.50	21.81	4.24	49.01
1993	249,086	710.64	606.28	807.54	26.63	5.17	59.83
1994	225,646	643.77	549.22	731.54	24.12	4.68	54.20
1995	218,735	624.05	532.40	709.14	23.38	4.54	52.54
1996	194,173	553.98	472.62	629.51	20.76	4.03	46.64
1997	168,826	290.04	234.33	344.41	45.58	28.21	65.49
1998	172,478	296.32	239.40	351.86	46.57	28.82	66.90
1999	157,933	271.33	219.21	322.18	42.64	26.39	61.26

Introducing some elements of uncertainty in the inputs highlighted the large variability of the bycatch estimates (see the values obtained for the lower and upper CI [confidence intervals]; Table 4.). However, even including uncertainty in the inputs, these values remained very low compared with bycatches reported from other fisheries. Based on these results, the total bycatch of billfishes taken by the entire purse-seine fleet operating in the eastern Atlantic was tentatively estimated. This calculation is supported by the facts that 1) the European fleet is the main component of the purse-seine fishery operating in this part of the ocean and 2) it is reasonable to assume that other fleets of purse seiners adopted the same fishing strategies as the European fleet. With this approach, the ratio of the billfish bycatch per tons of tunas (obtained from the European fleet; Table 3) was raised to the total tuna catch taken by the entire purse-seine fishery (Table 4). To account for the change in fishing strategies caused by the ban on FAD fishing operations, we performed new billfish ratio estimates for the years 1997, 1998, and 1999. These results give an indication of the bycatch of billfishes in the eastern Atlantic purse-seine fishery (Table 4).

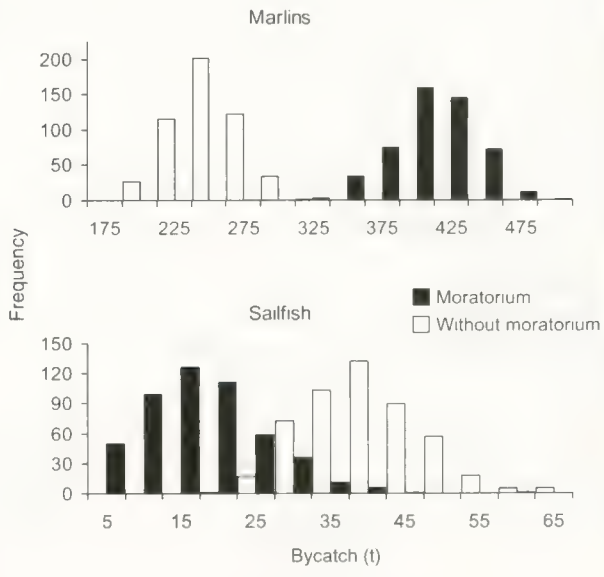

Figure 5

Histograms of Monte-Carlo-generated total billfish bycatch (marlin group in the upper histogram and sailfish group in the lower histogram) taken by the European Union tuna purse-seine fishery, taking into account whether a moratorium on FAD fishing was applied or not, in the eastern Atlantic Ocean.

Discussion

The ecosystem approach to assessing and managing large coastal marine ecosystems has been developing since the early nineties (Sherman and Duda, 1999). To date, with the exception of the central Pacific Ocean (Kitchell et al., 1999), this approach generally has not been used for monitoring large pelagic fisheries in offshore waters. Our study, in presenting data on bycatch of billfishes taken by the tuna purse-seine fishery, helps to extend this approach to the monitoring of the eastern Atlantic epipelagic ecosystem.

A purse-seine fishery cannot be assessed purely in terms of the tuna catch. In the eastern Atlantic Ocean, it can be assumed that the large catches of tunas taken by the purse seiners (around 200,000 t per year in the last decade, Table 4) affect the abundance of billfishes 1) directly, by generating bycatch and 2) indirectly, by increasing or decreasing

the abundance of predators or competitors, thereby changing the ratio of predators to prey in the trophic chain.

That the bycatch of Istiophoridae represents less than 0.021% of the total tuna catch and less than 10% of the total catches of billfishes currently reported for the eastern Atlantic Ocean (assumed to fluctuate around 7000–8000 t per year) suggests that the direct impact of the purse-seine fishery on these stocks is weak. By comparison, previous research has shown that the discards of small tunas and the total bycatch (billfishes, sharks, other fishes, etc.) generated by this fishery were close to 2% and 1.9%, respectively (Ariz and Gaertner, 1999). Compared with the longline fishery, the European tuna purse-seine fishery generates less bycatch of billfishes than the longline fisheries targeting tuna (Matsumoto and Miyabe, 2000; Gonzalez Ania et al., 2001), swordfish (Mejuto et al., 2000), or both species (Cramer, 2000; Marcano et al., 2000).

One of the more general implications of our findings concerns the impact of the ban of FADs by the purse-seine fishery on the bycatch of Istiophoridae. Our analysis suggests that this moratorium led to a decrease in incidental catch of marlin from 600–700 t to less than 300 t. In contrast, this trend was reversed for sailfishes, but the corresponding bycatch increased only from 25 t to 45 t. Because in the present study we did not take into account different probabilities (see Table 1) for each strata, it could be argued that the Monte Carlo simulations lead to only a partial exploration of the uncertainty in the calculation of the total billfish bycatch. However, it would be interesting to consider this source of uncertainty in the future. Consequently, the potential for possible regulations at different spatial and temporal scales needs further exploration.

Large bycatches of billfishes could affect the food web of the epipelagic ecosystem inhabited by other apex predators. However, the "zero bycatch solution" propounded by some environmentalist groups could accelerate the change in biomass ratios between the different trophic levels of the ecosystem. In a critique of the conventional risk factors (e.g. biological reference points) used to define the risk of extinction in marine fishes, Musick (1999) introduced other interesting criteria, such as rarity of a species, the small distribution range of a species, endemic species, and specialized habitat requirements. As can be seen in Figures 1–4, the range of spatial distribution of the billfishes is very large. It could be argued that billfishes are relatively widespread but occupy very specific habitats within their range, and as a consequence, habitat loss could be examined as a risk factor. However there is no clear evidence to support this hypothesis for billfishes.

The difficulty of objectively measuring an ecological risk when it concerns unexploited components of the ecosystem must be stressed because of the vagueness of this concept (Antoine et al., 1998). As a consequence, estimating the ecological risk is reduced to the analysis of the impact of a fishing practice on a limited number of symbolic species (e.g. dolphins, sea turtles; Hall, 1996). Nevertheless, there is no reason to believe that these charismatic species play a larger role in the food web of the epipelagic ecosystem than other targeted or nontargeted species. As shown by Kitchell et al. (1999), there was no clear conclusion on the ecological role of apex predators (including billfishes) in foods webs of the central North Pacific. Furthermore, if a decision is made to reduce the ecological impact of the bycatch in a given fishery, management actions cannot be focused only on providing full protection for a single species (Hall, 1996). Although everybody understands what "ecosystem overfishing" means, Murawski (2000) highlighted the lack of consensus for defining this concept and suggested the need for objective metrics that gauge properties associated with the main features of the ecosystem (e.g. production, diversity, and variability).

In addition, decision makers need to evaluate management options that are both scientifically credible and economically practical regarding the use of the ecosystems. Because billfishes are sold on the local African fish market (Romany et al., 2000), the effects of the fishing on the ecological processes, as well as on human activities, must be evaluated. Although in the past the regulatory process did not account for sharing of gains nor the social costs associated with fishing practices (Antoine et al., 1998), evidence suggests that the ecosystem approach for managing marine resources should also include these socioeconomic considerations in a multicriteria analysis (Chesson et al, 1999, Sherman and Duda, 1999).

Conclusion

This study examined the bycatch taken by the European tuna purse-seine fishery in the eastern Atlantic Ocean. Results obtained from this fleet have been extrapolated to the entire purse-seine fleet operating in the same areas of this ocean. The main conclusion of this paper is that the direct impact of the purse-seine fishery on the billfish component of the epipelagic ecosystem is weak. Results of this study provide additional information on the effect of the moratorium on FAD fishing. Although some caution is required at this stage, due to limitations of the spatial and temporal sampling coverage, it was found that the ban on FAD fishing operations led to a substantial decrease in marlin bycatch.

The present state of knowledge allows us to reach only preliminary conclusions. However, it should be borne in mind that inadequate data can lead to the formation of misguided policies. It is clear that detailed information on bycatch is needed to counter the arguments of those who propose total bans on some fishing practices. Consequently tuna commissions must continue to pay attention to the collection of bycatch statistics and must encourage fishermen to report incidental catches in their logbooks, at least by large taxa (e.g. billfishes, sharks, etc.). In order to use accurate information for management purposes, we recommend that data from regularly conducted observer programs be used as part of any future research.

Acknowledgments

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by the European purse-seiner tuna fleets in the Atlantic Ocean." This study would not have been possible without the help of the Spanish and French tuna companies and the skippers and crews who accepted observers aboard.

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Life history of South African snoek, *Thyrsites atun* (Pisces: Gempylidae): a pelagic predator of the Benguela ecosystem

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Abstract—Snoek (*Thyrsites atun*) is a valuable commercial species and an important predator of small pelagic fishes in the Benguela ecosystem. The South African population attains 50% sexual maturity at a fork length of ca.73.0 cm (3 years). Spawning occurs offshore during winter–spring, along the shelf break (150–400 m) of the western Agulhas Bank and the South African west coast. Prevailing currents transport eggs and larvae to a primary nursery ground north of Cape Columbine and to a secondary nursery area to the east of Danger Point; both shallower than 150 m. Juveniles remain on the nursery grounds until maturity, growing to between 33 and 44 cm in the first year (3.25 cm/month). Onshore–offshore distribution (between 5- and 150-m isobaths) of juveniles is determined largely by prey availability and includes a seasonal inshore migration in autumn in response to clupeoid recruitment. Adults are found throughout the distribution range of the species, and although they move offshore to spawn—there is some southward dispersion as the spawning season progresses—longshore movement is apparently random and without a seasonal basis. Relative condition of both sexes declined dramatically with the onset of spawning. Mesenteric fat loss was, however, higher in females, despite a greater rate of prey consumption. Spatial differences in sex ratios and indices of prey consumption suggest that females on the west coast move inshore to feed between spawning events, but that those found farther south along the western Agulhas Bank remain on the spawning ground throughout the spawning season. This regional difference in female behavior is attributed to higher offshore abundance of clupeid prey on the western Agulhas Bank, as determined from both diet and rates of prey consumption.

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Snoek (*Thyrsites atun*) is a medium-size, pelagic predator (max. size 9 kg; Nepgen, 1979a) inhabiting the coastal waters of the temperate Southern Hemisphere; it is found from the surface to the seabed, to depths of 550 m (Kailola et al., 1993). Occurring off southern Africa, Australia, New Zealand, the east and west coasts of southern South America, Tristan da Cunha, and the islands of Amsterdam and St. Paul (Nakamura and Parin, 1993), snoek have successfully colonized environments as diverse as oceanic island, west coast upwelling, and subtropical convergence ecosystems. It is an important food fish throughout much of its distribution, supporting moderate fisheries (<1000 metric tons [t]/yr) off southern Australia, Chile, and Tristan de Chuna, and substantial fisheries (>10,000 t/yr) off New Zealand and Southern Africa (Andrew et al., 1995; FAO, 1997).

Southern African snoek have been recorded from northern Angola to Algoa Bay on the South African east coast but are mostly found between the Cunene River and Cape Agulhas, i.e. in the Benguela ecosystem. *Thyrsites atun* has been an important commercial species in this system since the early 1800s, caught initially with hand lines but also trawled after 1960 (Crawford, 1995). Total catch peaked at about 81,000 t in 1978 but dropped substantially with the exclusion of foreign trawlers from the Namibian fishing grounds in 1991 (FAO, 1978, 1981, 1990, 1997). Current annual-catch ranges between 14,437 and 22,920 t (1991–95), and 93% of it is made in South African waters (FAO, 1995). *Thyrsites atun* is far the most important species caught by the South African commercial line fishery[1] (comprising 39% of the 1986–97 catch [National Marine Linefish System[2]]); it is also targeted by recreational anglers, for which catch statistics are not available. Around 40% of the South African catch (1990–96) is made by commercial handline fishermen and 60% by trawlers (Demersal Commercial Data Base[3]). However, the commercial line-catch may be under-reported by as much as 75% (Sauer et al., 1997); therefore the total catch could be substantially larger. In addition to its fishery significance, *T. atun* is a major predator of anchovy (*Engraulis japonicus*) and sardine (*Sardinops sagax*) in the southern Benguela ecosystem (Wickens et al., 1992) and has been implicated in top down effects on both prey and consequently zooplankton populations (Verheye et al., 1998).

Life-history information is fundamental to identifying and assessing fish stocks, as well as to formulating management strategies for their sustainable use. Whereas snoek stocks off Australia (Blackburn and Gartner, 1954; Blackburn, 1957; Grant et al., 1978) and New Zealand (Mehl, 1971;

[1] The South African commercial linefishery consists of about 2500 vessels (5.5–15 m long) that operate on the continental shelf using handline or rod-and-reel.

[2] National Marine Linefish System. 2000. Unpubl. data. Linefish Section, Marine and Coastal Management, Private Bag X2 Roggebaai 8012, Cape Town, South Africa.

[3] Demersal Commercial Data Base. 2000. Unpubl. data. Demersal Section, Marine and Coastal Management, Private Bag X2 Roggebaai 8012, Cape Town, South Africa.

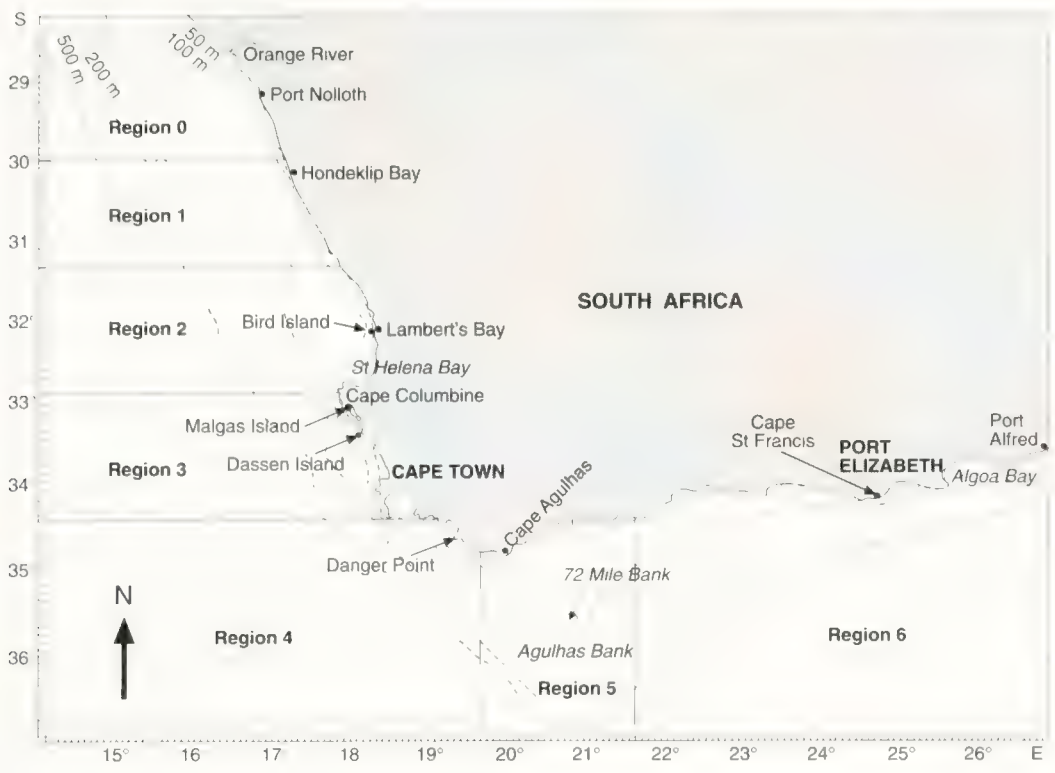

Figure 1

Map of the seven regions in which snoek (*Thyrsites atun*) were sampled, and the localities mentioned in the text. Snoek caught by hook and line were, with the exception of the 72-mile bank (region 5), taken within 15 km of the coastline, whereas those that were trawled were caught farther from the shore at water depths between 150 and 600 m.

Hurst, 1988; Hurst and Bagley, 1987; 1989) have been extensively studied, knowledge of the life history of the Benguela snoek is surprisingly fragmented, in spite of its socioeconomic and ecological importance and long history of exploitation. An extensive seasonal migration between the northern and southern regions of the Benguela system has been postulated (Davies, 1954; Crawford and De Villiers, 1985; Crawford et al., 1987); however, this migration was based largely on anecdotal reports of line catches and remains to be confirmed. Preliminary observations of gonad maturity (Davies, 1954; Nepgen, 1979a) and trends in the abundance of eggs and larvae (Olivar and Fortuño, 1991; Olivar and Shelton, 1993) suggest that spawning occurs in winter and spring, but the spawning season has not been accurately described. Three previous studies on the diet of snoek in South African waters (Nepgen, 1979b, 1982; Dudley, 1987) excluded juveniles (<75 cm fork length) because nursery grounds were not sampled, and inadequate sample sizes precluded meaningful comparisons of snoek offshore and closer to the coast, and spatial comparisons of offshore diet.

The objective of this study was to provide information on the life history of South African *T. atun*, including season and localities of spawning, condition, nursery areas, juvenile growth, size-at-maturity, diet, and patterns of juvenile and adult distribution.

Materials and methods

The South African coastline between the Orange River and Cape St Francis was divided into seven sampling regions (Fig. 1). Biological (September 1994–January 1998) and length-frequency (January 1985–December 1997) data were collected in each region from fish caught by 1) the line fishery, 2) the demersal trawl fishery, and 3) research trawl surveys of pelagic and demersal fish conducted by Marine and Coastal Management. The trawl fishery operates farther offshore than the line fishery; consequently all fish sampled deeper than 150 m were trawl caught, whereas the bulk of those from shallower depths were caught by hook and line (except for a small number caught by trawl during research cruises).

Demersal biomass surveys (DBS), based on the swept-area method, are designed to provide annual indices of biomass for the resources exploited by the South African hake-directed trawl fishery, and methods have been fully described by Badenhorst and Smale (1991). DBSs are subdivided into two areas: the Namibian border to Cape Agulhas (west coast), and Cape Agulhas to Port Alfred (south coast). In each survey, area was divided into four depth zones (0–50 m, 51–100 m, 101–200 m, and 200–500 m) which, in turn, were subdivided into blocks of 5 × 5 nautical miles. The blocks trawled each survey were

determined semirandomly according to the ratio of blocks per stratum. Bobbins were not used, so that trawling was limited to nonreef substrata. A 180-foot German trawl was used with 25-mm mesh (bar) liner attached to the bag. Trawl duration was limited to 30 minutes; results of shorter trawls (caused by technical reasons or to hitting reef) were standardized to that time. Winter and summer cruises were undertaken on the west coast between July 1985 and January 1991; and autumn and winter–spring cruises on the south coast between September 1987 and April 1996.

Pelagic biomass surveys (PBS) are hydroacoustic surveys designed to estimate annual spawner biomass and recruitment strength of small, pelagic clupeoids—*E. japonicus*, *S. sagax*, and round herring, *Etrumeus whiteheadi* (see Hampton, 1992, for details). Acoustic targets are identified by directed trawling with an Engels 308 midwater trawl fitted with a codend liner of 8-mm mesh. Small *T. atun* (<30 cm) shoal with the pelagic species while larger individuals feed on them. As a result snoek are regularly caught by trawl on PBSs, albeit in small numbers (<30 per trawl). These surveys provide qualitative data on the distribution of juvenile snoek. A total of 80 PBSs, including more than 1500 midwater trawls, were completed between 1985 and 1997. Although the survey area varied considerably, with the extremes being Lüderitz (26°39′S; 15°09′E) in southern Namibia and Cape St Lucia (28°31′S; 32°25′E) in northern KwaZulu-Natal, regions 0–5 of the present study were consistently covered.

Migration of *T. atun* was studied by using spatial and temporal variation in magnitude and size composition of catches. Owners of commercial line boats and trawlers are required to submit daily catch returns to Marine and Coastal Management (MCM). The monthly catches of snoek reported by the trawl and line fisheries in each of the seven regions (1986–97) were expressed as percentages of the respective annual totals. Mean monthly handline catch per unit of effort (kg/boat/day) and trawl CPUE (kg/hour) by 50-m depth zones were calculated for each region. Catch rates recorded during fishery-independent DBSs were mapped separately for summer and winter cruises and presented as mean numbers of snoek per 30-min trawl, per grid block.

Fish sampled for biological purposes were measured to the nearest 1 mm (fork length), weighed, to the nearest gram (fish <500 g), or the nearest 10 g (fish >500 g), cut open, and sex was determined. Gonads were removed, assigned a macroscopic index of maturity (see Table 1), and weighed to the nearest 0.1 g. Random samples (n=5–30) of each macroscopic ovarian stage were fixed in Bouins solution for 48 hours and then stored in 70% ethanol for microscopic verification. They were routinely embedded in paraffin wax, sectioned to 3–7 µm, and stained with haemotoxylin and eosin. Stomach contents were analyzed fresh, and prey items were identified to the lowest possible taxon and weighed (wet) to the nearest 0.1 g. Bait was recognized easily and discarded.

The size at 50% maturity (L_{50}) for males and females was estimated by PROBIT analysis (SPSS, 1992) of the fractions of mature fish (gonad stage 3+) per 5-cm length class (midpoint), sampled during the breeding season. Upper and lower 95% confidence limits were calculated by the software package by using maximum-likelihood estimation.

Seasonal patterns of reproduction were established by calculating gonadosomatic indices (GSIs) and the monthly percent frequency of each maturity stage, for fish $>L_{50}$:

$$GSI = gonad\ weight / \left(\begin{bmatrix} fish\ weight - \\ gonad\ weight + \\ stomach\ content\ weight \end{bmatrix} \right) \times 100.$$

The extent of the spawning area was determined by computing the percent frequency of each maturity stage for females ($>L_{50}$) that were sampled in each region during peak spawning (June–October). Snoek spawn on the trawl grounds (see below); thus spawning grounds were further delineated by mapping commercial trawl CPUE (standardized by using general linear modelling to account for vessel size) during June–October (1986–97) with a 20 × 20 mile grid system. Commercial trawl CPUE was also used to establish the depth distribution of snoek on the trawl grounds, and hence the depth of the spawning area. Sex ratios were tested statistically for significant deviations from equality with chi-square tests.

Nursery areas were delineated by comparing the length-frequency distributions of snoek caught in each region 1) during pelagic and demersal biomass surveys, 2) by the line fishery, and iii) by Cape gannets, *Morus capensis*. Because trawling activities during PBSs were aimed at small pelagic clupeoids, it was not possible to use CPUE data from these cruises to analyze spatial patterns in juvenile snoek abundance. However, gannets from Lambert's Bay and Malgas Island (Fig. 1) have feeding distributions that, although large, are separated at Cape Columbine and do not overlap to any large extent (Berruti, 1987). Previous studies (Crawford et al., 1992; Berruti et al., 1993; Crawford, 1998) have demonstrated that gannet diet adequately reflects temporal and spatial patterns in prey abundance. Relative abundance of early-juvenile snoek north and south of Cape Columbine was therefore estimated by comparing rates of snoek consumption by the two colonies. Stomach contents of gannets at the two colonies have been sampled on a monthly basis since 1978 (see Berruti et al., 1993, for methods). Lengths of snoek prey were obtained from undigested specimens, and snoek consumption by the two colonies was compared annually (1978–97) using the mean mass per stomach containing food and percentage frequency of occurrence (i.e. percentage of stomachs with food that contained snoek).

Dietary importance of snoek prey was assessed by percentage frequency of occurrence (%F), which provides an indication of how often a particular item is selected within a population (Hynes, 1950), and by percentage by mass (%M) (Windell and Bowen, 1978), a measure of the energy contribution of that item (Macdonald and Green, 1983). An index of relative importance (*IRI*) was calculated for each prey category i as the product of $\%M_i$ and $\%F_i$. To facilitate comparisons of prey importance between analyses (e.g. separated spatially, temporally or according to predator size), this was expressed as a percentage (Cortés, 1997):

Table 1

Description of gonad maturity stages of snoek (*Tyrsites atun*) in South African waters. Microscopic descriptions are given only for females.

Stage	Macroscopic appearance	Microscopic appearance
1 Immature and resting	Ovaries appear as clear, pinkish, or translucent orange tubes. Eggs are not visible to the naked eye. Testes thread-like and clear, to ribbon-like and pinkish white in color.	Some ovaries in this stage consist entirely of primary growth oocytes and others contain oocytes to the early cortical alveoli stage. α atresia of unyolked and β atresia of yolked oocytes are also observed.
2 Active	Eggs discernible to the naked eye as yellow granules that do not occupy all available space in ovary. There is very little increase in the diameter of the ovary. Testes are wider, triangular in cross-section, and beige or cream in color. Sperm is present if the gonad is cut and gently squeezed.	Primary growth to early yolked oocytes evident. Those at the end of the spawning season show a high degree of α atresia.
3 Ripe	Ovaries completely opaque and orange to yellow in color. They are larger in diameter and eggs occupy all available space. Testes still larger in cross-section and softer in texture. They become creamier in color due to considerable quantities of sperm.	Primary growth to late yolk-stage oocytes present. Atresia and postovulatory follicles evident in some.
4 Ripe or running	Ovaries considerably larger in diameter, amber in color with a substantial proportion of hydrated eggs. Sperm is freely extruded when pressure is applied to the abdomen of the whole fish.	All stages from primary growth to hydrated oocytes present.
5 Spent	Ovaries are reduced in size, similar in appearance to stage-1 ovaries, and have a few yolked oocytes remaining. These yolked oocytes are generally aspherical and appear to be undergoing resorption. Testes are shrivelled in appearance and mottled beige and cream in color. A little viscous semen may still ooze from the genital pore when pressure is applied to the abdomen.	Primary growth to advanced yolk-stage oocytes present, but a much lower proportion of yolked oocytes than in previous stages; major atresia of yolked oocytes also present.

$$\%IRI_i = 100IRI_i / \sum_{i=1}^{n} IRI_i,$$

where n = the total number of food categories considered at a given taxonomic level.

Numerical percentage contribution (Pillay, 1952) was excluded because *T. atun* has a diverse diet and this method would bias the results towards small crustaceans, e.g. euphausiids and amphipods, which are not individually selected. Inshore samples for dietary analysis were collected from the west coast (regions 1–3) while offshore samples were collected from both the west coast (regions 1–3) and western Agulhas Bank (regions 4 and 5).

Proportion of stomachs containing food and the mean mass of stomach contents (including fish with empty stomachs) were used as indices of the rate of prey consumption for adult (≥75 cm) snoek. Sexual and spatial differences were tested for statistical significance by using chi-square tests (2 × 2 contingency tables) for frequency data (i.e. numbers with and without food), and a two-way ANOVA with single observations for mean prey mass data.

Monthly relative condition (Kn) was calculated for adult snoek (≥75 cm) as follows:

$$Kn_j = \frac{\sum_{i}^{n} \frac{w_i}{aFL_i^b}}{n_j},$$

where W_I = the gonad and stomach content free weight (g) of the i^{th} individual in the j^{th} month;
FL_i = the fork length (mm) of the i^{th} individual;
a (0.000018) and b (2.80) are constants from the length-weight (gonad and stomach content free) relationship derived from data collected during the present study (all months combined); and
n_j = the number of fish sampled in the j^{th} month.

Snoek accumulate fat as three longitudinal mesenteric deposits along the outer walls of the stomach. Monthly

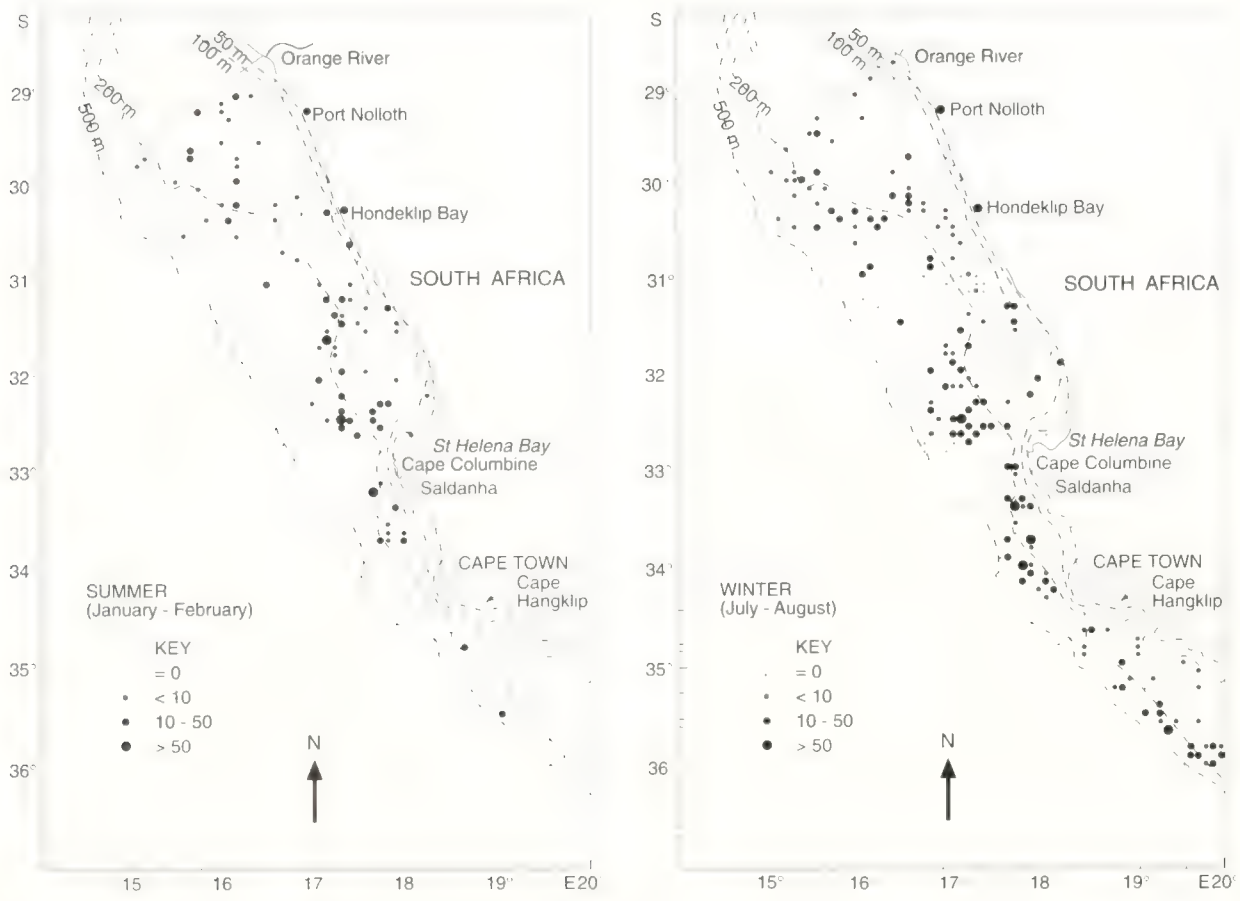

Figure 2A

Mean number of *Thyrsites atun* per trawl per grid block (5 × 5 nmi) by season for (**A**) the west coast (July 1985–Jan 1991; n=18 surveys and 1624 trawls) and (**B**) the south coast (September 1987–April 1996; n=18 surveys and 1554 trawls) demersal biomass surveys off South Africa.

proportions of stomachs with no fat were calculated separately for adult (≥75 cm) males and females.

Results

Migration

Spatial analysis of CPUE from fishery-independent DBSs indicated that *T. atun* are distributed farther offshore and farther southeast in winter and spring than in summer and autumn (Fig. 2). Fishery-dependent data support this pattern; commercial catches from the trawl grounds (i.e. >150 m) were highest from June to October, and those in the southern regions (3–6) lagged behind catches in the north (regions 0–2) by approximately one month (Fig. 3). Analysis of trawl CPUE by depth, area, and season (Fig. 4) further confirmed offshore movement during the spawning period (June–October) and furthermore revealed that *T. atun* were most abundant between bottom depths of 150 m and 350 m while on the trawl grounds. Snoek found on the trawl grounds were generally >65 cm FL (Fig. 5A).

Line-based catch and CPUE in regions 0–2 was distinctly seasonal; most of the catch was made from April to June (Fig. 3) and a slight southwards progression in peak catch and CPUE occurred within this period (Fig. 3). Line-caught snoek from regions 1 and 2 were substantially smaller (50–75 cm) and younger (1–3 years; author, unpubl. data) than those from region 3 (80–95 cm; 3–7 years) (Fig. 5B).

Line-caught snoek in region 3 were mostly >L_{50} (Fig. 5B). Monthly catch and CPUE statistics from this region depicted no trend, indicating that adult snoek are available to line fishermen throughout the year (Fig. 3). Catch rates in region 4 were highest between July and October, which is consistent with the winter–spring south–eastward dispersal of adult snoek evident from trawl data (above). Handline catch and CPUE in regions 5 and 6 were highest during the first half of the year but declined dramatically in winter.

Size at maturity

The ratio of active (stage-2) to ripe (stage-3) ovaries during the spawning season decreased with fish length

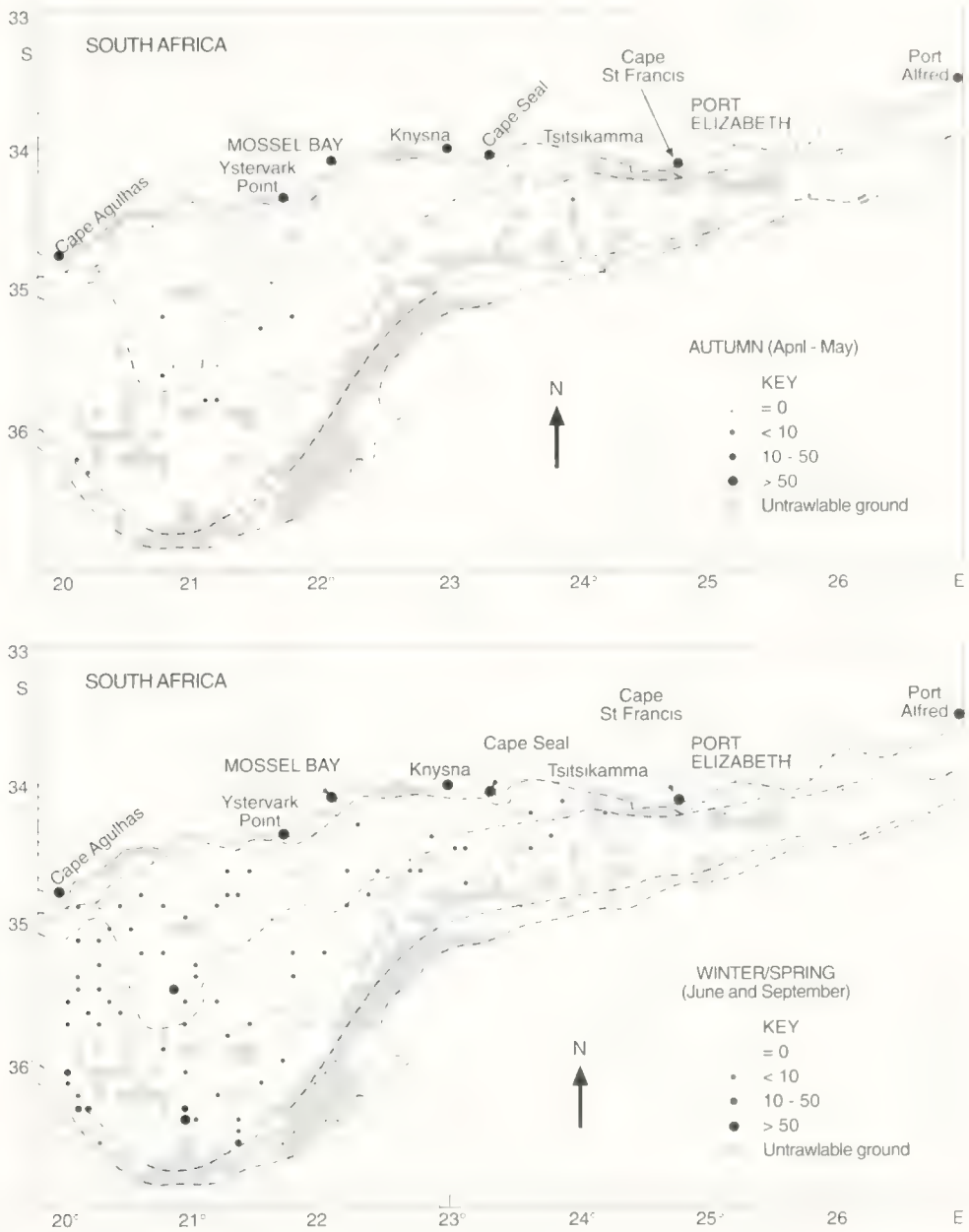

Figure 2B

(Fig. 6A), suggesting (as in other teleosts; Griffiths and Hecht, 1995) that substantial proportions of snoek in the smaller size classes undergo partial gonad development during the season prior to maturity. Because these fish are unlikely to spawn, only specimens with gonads developed to at least stage 3 (ripe) were regarded as mature. Given that snoek spawn offshore (see below) and that almost all fish on the trawl grounds (regardless of size) were mature (Fig. 6B), L_{50} maturity calculations were limited to fish sampled inshore (<150 m)[4]: 72.0 cm for males and 73.4 cm for females (Fig. 7). Upper and lower 95% confidence limits were 69.3 and 74.3 cm for males, and 71.3 and 75.4 cm for females. L_{50} for combined male and female data was 73.0 cm with 95% confidence intervals of 70.0 and 75.2 cm. In all cases the L_{50} values corresponded with an age of 3 years (author, unpubl. data).

[4] In situations where fish migrate to spawn, all fish on the spawning ground are mature. As a result, even if 10% of a particular size class (x–y cm) in the population are mature, the sampling of that 10% once it had migrated onto the spawning grounds would suggest that 100% of that size class are mature. Because mature snoek move back and forth between the spawning and feeding grounds (offshore and inshore) in regions 0–3 during the spawning season, and could readily be distinguished from immature fish, inshore samples were used to determine size at maturity.

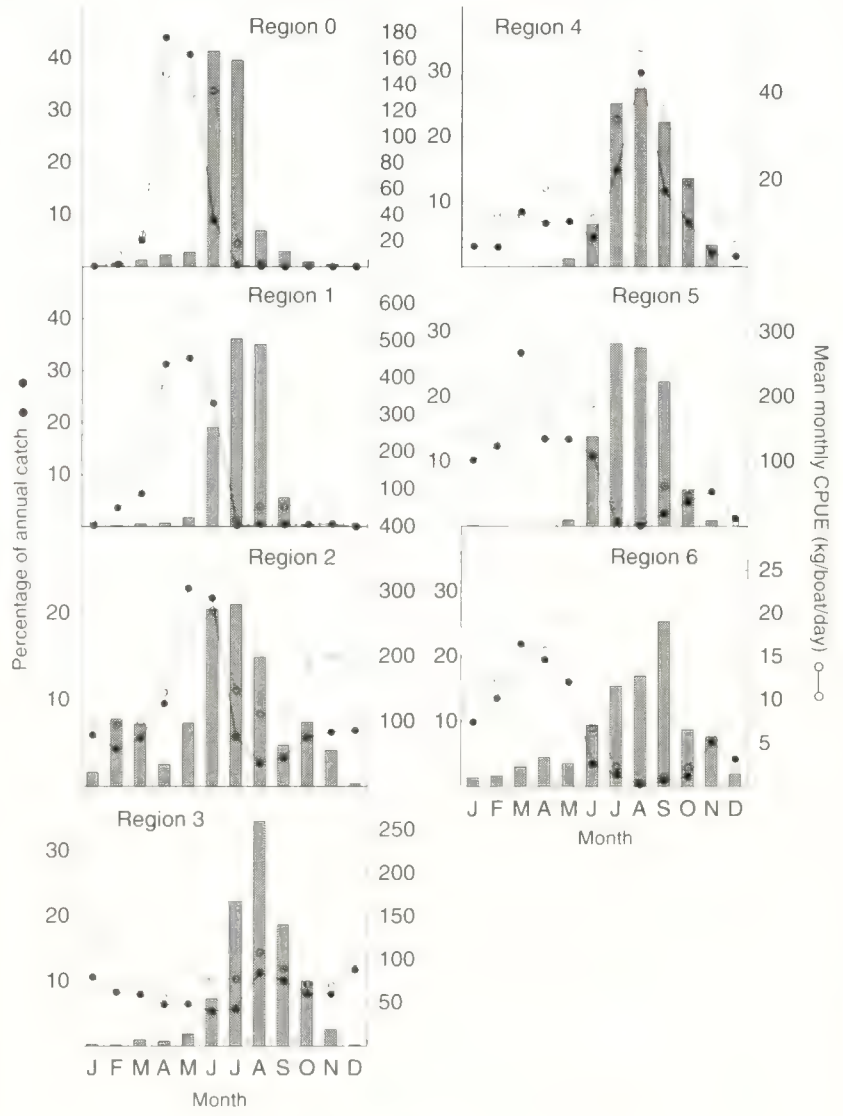

Figure 3

Catches of *Thyrsites atun* made by South African commercial trawlers (bars) and line fishermen (black circles) summed on a monthly basis in each region and expressed as percentages of the total catch for the period 1985–1997. Mean monthly catch per unit of effort (kg/boat/day) of *T. atun* caught by South African commercial line fishermen in each region (open circles) is also given (1985–97). Because the bulk (70 %) of the line catch in region 5 was made on offshore pinnacles (i.e. over a 72-mile bank), the CPUE trend for this region was based on data from this area. The offshore pinnacles (the 72-mile bank being the deepest) are, however, located well inshore of the trawl grounds in that region (see Fig. 1).

Spawning

Gonadosomatic indices (Fig. 8) and gonad maturity indices (Fig. 9) showed that South African snoek spawn from May to November and that peak spawning occurs from June to October (winter–spring). Monthly male GSIs were similar inshore and offshore, but female values were higher offshore during the spawning season. In addition, a substantial proportion (20+%) of offshore females in regions 2 to 5 had hydrated oocytes (stage 4), whereas this gonad stage was rarely observed inshore. Spatial patterns in trawl CPUE from both fishery-independent (Fig. 2) and fishery-dependent (Fig. 10) data collected during winter–spring suggest an extensive spawning ground that encom-

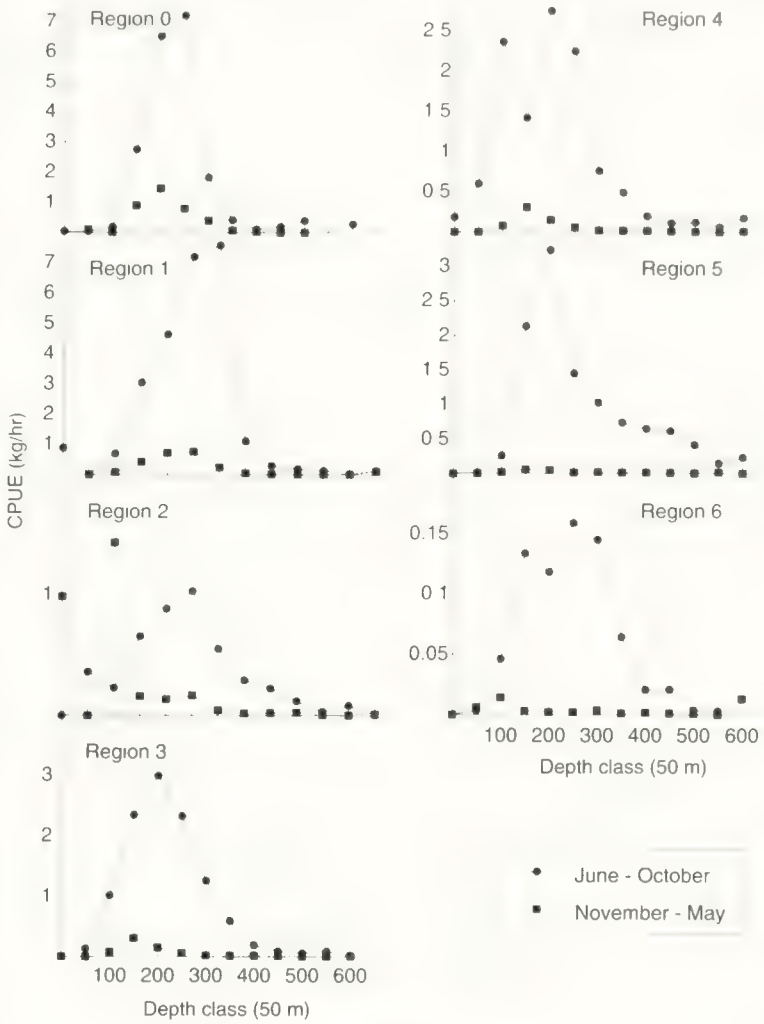

Figure 4

Catch per unit of effort (CPUE; kg/h) per 50-m depth category for *Thyrsites atun* commercially bottom trawled in each of the seven regions during winter–spring and summer–autumn, 1986–97.

passed the western edge of the Agulhas Bank and most of the South African west coast, to a point just north of Hondeklip Bay.

The predominance of ripe (stage-3) females (both inshore and offshore) throughout the protracted spawning season (Fig. 9) is indicative of multiple spawning (Griffiths, 1997). Moreover, the simultaneous occurrence of postovulatory follicles (POFs) with both primary growth and advanced yolked-stage oocytes (Fig. 11) confirmed that snoek are indeterminate, serial spawners.

Sex ratio

Sex ratios in regions 0–3 were skewed towards females inshore and males offshore (Table 2), a pattern most pronounced during the spawning season (winter–spring). Inshore, this pattern was most evident in the adult size class (≥75 cm). Adult sex ratios in regions 0–3 during the spawning season were 2.9F:1M inshore and 1F:2M offshore. Inshore and offshore sex ratios of adult snoek in regions 4 and 5 (Table 2) revealed no clear pattern; although moderately more females were sampled on the trawl grounds of these regions during the spawning season (1.6F:1M), the inshore ratio (1M:1.2F) did not deviated significantly from unity.

Nursery areas

Monthly length-frequency distributions comprised fairly discrete modes in spite of variation in collection method and sampling period and clearly depicted early juvenile growth (Fig. 12). Young-of-the-year snoek first appeared

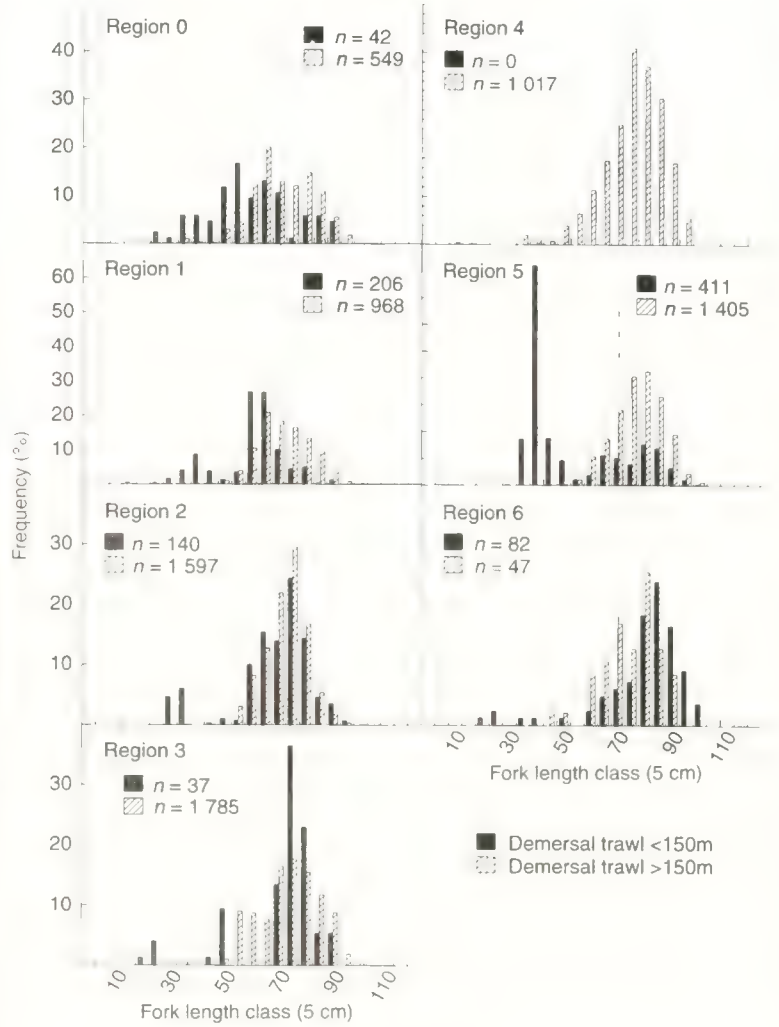

Figure 5A

Fork-length distributions of *Thyrsites atun* caught by (**A**) demersal trawl and (**B**) handline and midwater trawl in each region. Handline and midwater catches were made shorewards of the 150-m isobath and demersal catches were divided into those made deeper and shallower than this depth. The dotted line indicates length at maturity (L_{50}).

in the diets of gannets and in pelagic trawls during spring (Oct–Nov) at lengths 7–12 cm and grew rapidly to 33–44 cm by the spawning season (winter) of the following year (±3.25 cm/month). Early juveniles (<1 year old) were sampled (with fishing gear) in each of the seven regions (Fig. 5) but formed a larger proportion (by mass and frequency of occurrence) of the diet of gannets at Bird Island (Lamberts Bay) than in gannets of Malgas Island (Fig. 13). Snoek smaller than 70 cm comprised a far higher proportion of the handline and pelagic trawl catches of regions 0–2 than those from region 3 (Fig. 5B). Length frequencies of pelagic trawl, demersal trawl (<150 m), and line-caught snoek suggested that juveniles were also found in reasonable numbers to the east of Danger Point in regions 4 and 5. *Thyrsites atun* collected in demersal trawls deeper than 150 m were mostly >65 cm, whereas those from shallower bottom trawls included substantial proportions smaller than this length (Fig. 5A). Juveniles <30 cm, although present in pelagic trawls (Fig. 5B), were notably absent from demersal trawls, including those shallower than 150 m (Fig. 5A).

Diet

Snoek prey on a wide variety of demersal and pelagic organisms, including teleosts, crustaceans, and cephalopods (Tables 3 and 4) and show ontogenetic shifts. The diet of *T. atun* sampled inshore of the 150-m isobath along the west coast (regions 0–3) consisted predominantly of pelagic fishes, and crustaceans comprised a smaller but

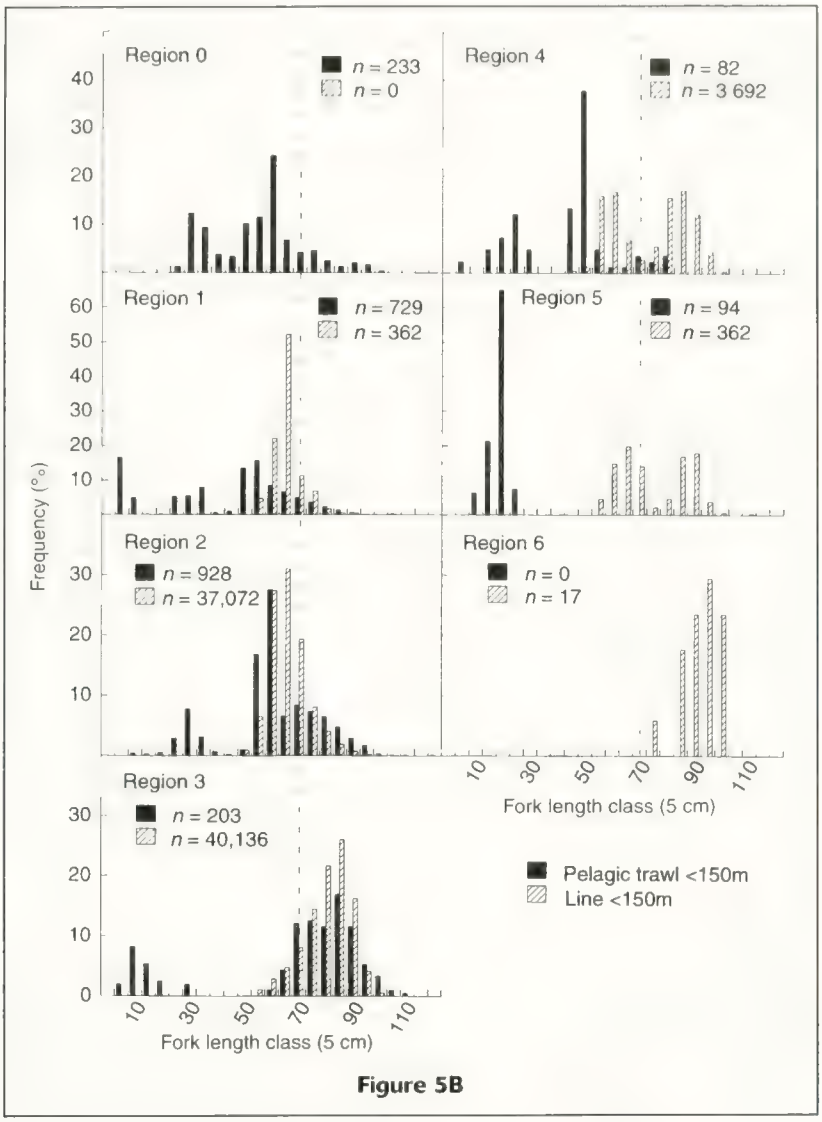

Figure 5B

Table 2

Inshore and offshore sex (M:F) ratios of *Thyrsites atun* during summer–autumn and winter–spring (spawning season) for the period 1994–97. Levels of significance—* ($P<0.05$), ** ($P<0.01$), and *** ($P<0.001$)—were determined by using a chi-square test (Yates' correction factor was applied as df =1).

	Inshore (<150 m)						Offshore (>150m)					
	Summer–Autumn			Winter–Spring			Summer–Autumn			Winter–Spring		
Fork length (cm)	M:F	*n*	χ^2	M:F	*n*	χ^2	M:F	*n*	χ^2	M:F	*n*	χ^2
Regions 0–3												
20–49	1:1	203	0.01	1:1.3	7	0						
50–74	1:1.2	647	4.5*	1:1.1	524	0.6	1.2:1	105	1.0	2.4:1	228	20.3***
>75	1:1.8	523	42.0***	1:2.9	1131	263.0***	1:1.2	134	1.3	2.0:1	704	61.3***
All sizes	1:1.4	1373	30.5***	1:2.0	1662	192.3***	1:1	241	0	2.1:1	933	82.3***
Regions 4–5												
20–49										1.3:1	7	0
50–74	1:1.1	53	0	1:1	24	0		No data		1:1	440	0
>75	1:2.0	6	0.1	1:1.2	46	0.2				1:1.6	586	31.1***
All sizes	1:1.2	59	0.4	1:1.1	70	0.1				1:1.3	1033	18.4***

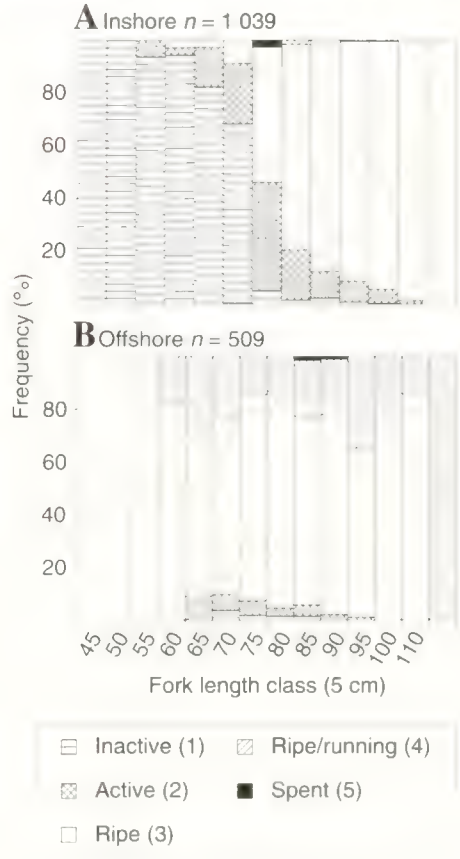

Figure 6

Percentage of macroscopic ovarian stages by 5-cm fork-length interval for *Thyrsites atun* sampled (**A**) inshore and (**B**) offshore (i.e. shorewards or seawards of the 150-m isobath) during the spawning season (June–October), 1994–97.

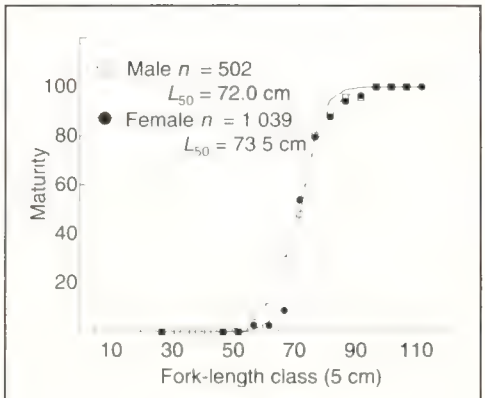

Figure 7

Percentage of mature (gonad stage 3+) *Thyrsites atun* by 5-cm fork-length class sampled during the spawning season (June–October), 1994–97. Symbols represent the observed data and the lines the fitted models. L_{50}= length-at-maturity (cm fork length); n = sample size.

noteworthy component that declined in importance with growth. In descending order. the most important prey items were as follows: lanternfish *Lampanyctodes hectoris* (IRI=46.5), euphausids *Euphausia leucens* (IRI=23), and the amphipod *Themisto gaudichaudi* (IRI=14.2) for early juveniles (5–24 cm); lanternfish (IRI=34.4), *T. gaudichaudi* (IRI=32.4), anchovies (IRI=2.8), and sardines (IRI=2.4) for juveniles (25–49 cm); anchovy (IRI=38.3), euphausids (IRI=26), and sardine (IRI=11.7) for subadults (50–74 cm); and sardine (IRI=47.4) and anchovy (IRI=38.6) for adults (≥75 cm).

In offshore waters snoek diet consisted almost exclusively of teleosts, including pelagic and demersal taxa. The most important prey items were sardine, round herring, and hake (*Merluccius* spp.) for snoek <75 cm; and hake, sardine and horse-mackerel (*Trachurus trachurus capensis*) for larger specimens. The main difference between the two offshore diets consisted in the greater importance of sardine (IRI=44.4 vs. 17.2 for snoek ≥75 cm) and the lesser importance of hake (IRI=31.8 vs. 60.8 for snoek ≥75 cm) off the western Agulhas Bank than off the west coast (Table 4). In both areas, large prey species, such as hake and horse mackerel, were more important in the larger (≥75 cm) size class.

Prey consumption

Both indices of prey consumption—proportions of stomachs containing food and mean mass of stomach contents—indicated that within each area and sampling season, adult females consumed more prey than adult males (Table 5); spatial and season trends were also evident. Two-way ANOVA with single observations revealed that differences in the mean mass of stomach contents between sexes (F= 65.9, df=1, $F_{critical}$=10.1) and between areas (F=215.5, df=3, $F_{critical}$=9.3) were both highly significant (P<0.001). Chi-square tests revealed that differences between the proportions of males and females with stomach contents were highly significant inshore on the west coast (WC) and offshore along the western Agulhas Bank (WAB) in winter–spring, but were not significant inshore on the WC in summer–autumn, or offshore on the WC in winter–spring (Table 5). Female mean stomach content mass was lowest (22.1 g) inshore on the WC in summer–autumn and highest (60.1 g) offshore on the WAB in winter–spring (spawning season). Female proportion with stomach contents was also lowest (52.5%) inshore on the WC in summer–autumn but highest (81.2%) in the same area during winter. Differences in female proportions with stomach contents between seasons inshore on the WC (χ^2=99.9, df=1), between inshore and offshore areas of the WC in winter–spring (χ^2=13.0, df=1) and between the offshore WAB and inshore WC during winter–spring (χ^2=26.3, df=1) were highly sig-

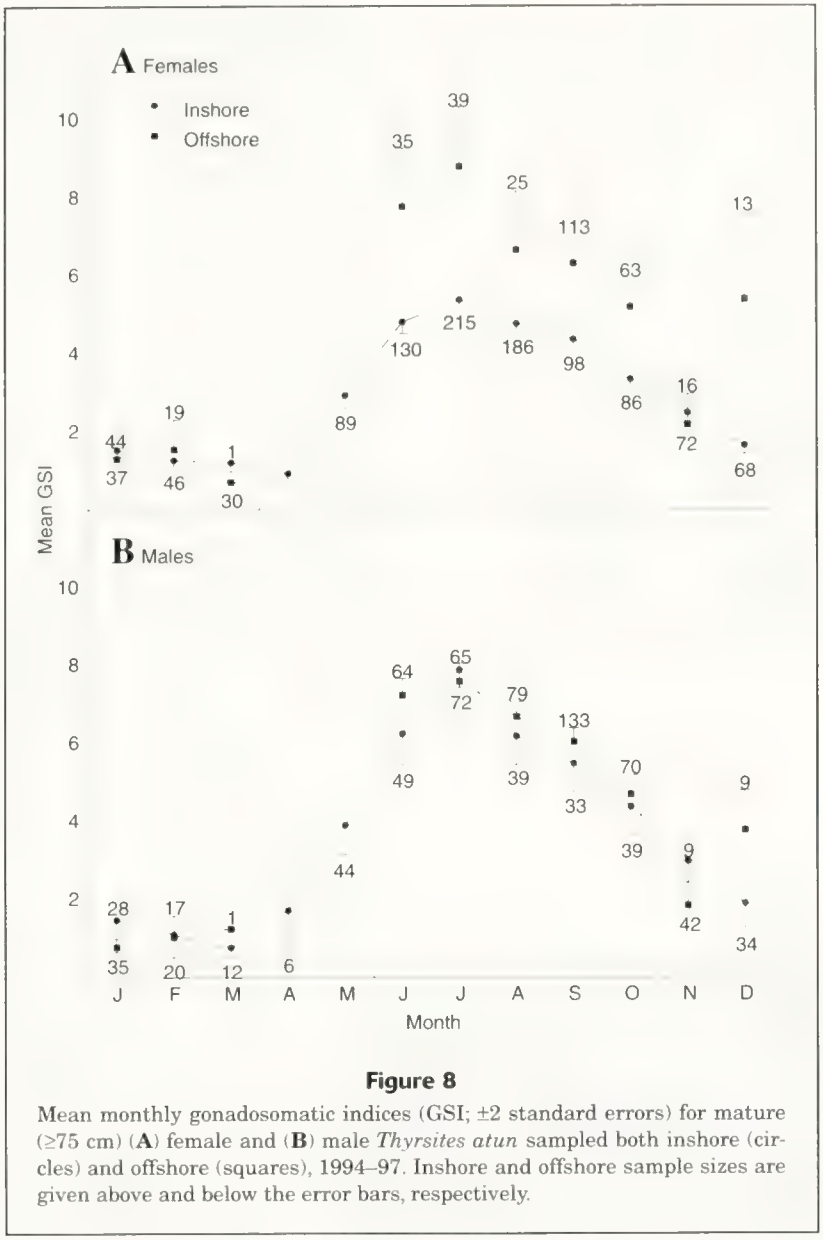

Figure 8

Mean monthly gonadosomatic indices (GSI; ±2 standard errors) for mature (≥75 cm) (**A**) female and (**B**) male *Thyrsites atun* sampled both inshore (circles) and offshore (squares), 1994–97. Inshore and offshore sample sizes are given above and below the error bars, respectively.

nificant ($P<0.01$), but differences between the two offshore areas—WC and WAB—in winter–spring were not. Mean stomach content mass was, nevertheless, substantially higher (60.1 g vs. 44.6 g.) offshore on the WAB than offshore of the WC during winter–spring (Table 5).

Condition

Relative condition (Kn) of adult snoek depicted a clearly seasonal cycle: highest between March and May, declining steeply through June to October (spawning season), increasing again from November through to March (Fig. 14). The proportion of stomachs without any fat was inversely related to Kn (Fig. 14): it was lowest from March to May but increased dramatically during the spawning season. The rate of fat decline was, however, higher in females than males; by September 90% of females and 58% of males had no mesenteric fat reserves.

Discussion

Crawford and De Villiers (1985) postulated that the snoek of the Benguela ecosystem comprise a single stock that undergoes a seasonal longshore migration—moving southwards into South African waters to spawn in winter and returning north, as far as southern Angola, in spring–summer. Although this theory has become widely accepted (Crawford et al., 1987; Crawford, 1995), this study showed that adult snoek are available to South African line fisher-

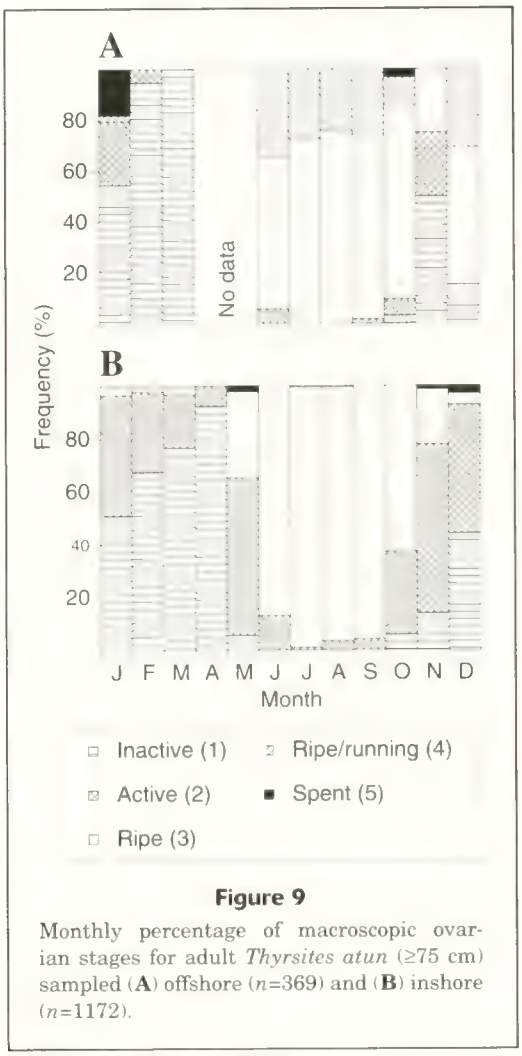

Figure 9

Monthly percentage of macroscopic ovarian stages for adult *Thyrsites atun* (≥75 cm) sampled (**A**) offshore (n=369) and (**B**) inshore (n=1172).

men throughout the year, and that the seasonal availability of adults on the trawl grounds results from an offshore spawning migration rather than southward movement from Namibian waters. Based on these results, *inter alia*, separate nursery areas and egg and larval distributions north and south of the cold upwelling cell (25–27°S) off southern Namibia, Griffiths (in press) concluded that Benguela snoek exist as two subpopulations, and have limited exchange.

The life history of South African *T. atun* is summarized by the conceptual model presented in Figure 15. Movement patterns were inferred largely from spatiotemporal trends in fishery-dependant catch and effort data. Considering that snoek is the most important line fish on the South African western seaboard and that it is a bycatch in the trawl fishery, catch trends are unlikely to have been biased by switches in targeting. Moreover, even though line-fish catches are under-reported (Sauer et al., 1997), they have been demonstrated to accurately reflect seasonal trends in the abundance of migratory species (Griffiths and Hecht, 1995). Given the offshore movement of adult fish during the spawning season and the associated ovarian condition (greater GSIs and the presence of hydrated oocytes), it is concluded that South African snoek spawn offshore between the 150- and 400-m isobaths. Although most of the inshore catch was line-caught, the absence of stage-4 females from trawls made shallower than 150 m during the spawning season (n=46, including 32 ripe [stage-3] specimens) indicates that this observation is not an artifact of gear selectivity. Spatial patterns in trawl CPUE from both fishery-independent (Fig. 2) and fishery-dependent (Fig. 11) data, collected during winter–spring, suggest an extensive spawning ground that encompasses the western edge of the Agulhas Bank and most of the South African west coast, to a point just north of Hondeklip Bay. Presence of snoek eggs and larvae (off South Africa) from the southern tip of the Agulhas Bank to Hondeklip Bay and their great abundance between the 200-m and 600-m isobaths (Olivar and Fortuño, 1991; Olivar and Shelton, 1993) corroborate offshore spawning and an extensive spawning ground. The occurrence of snoek preflexion larvae in region 6 (Wood, 1998) indicates that spawning does occur farther to the east, but the relatively low abundance of adult fish and spawning products suggests it is not an important spawning area.

The sex ratio of adults (≥75 cm) on the west coast (regions 0–3) was skewed towards males on the spawning grounds (2M:1F), and towards females further inshore (2.9F:1M), particularly during the spawning season. Based on the differential loss of intestinal fat, it is evident that the energetic demands of spawning are higher in females than in males. The higher rate of prey consumption by females during winter–spring (i.e. spawning season) than during summer–autumn and the greater prey consumption by females than by males during the spawning season indicate that they are able to enhance their spawning effort with exogenous energy. It is therefore postulated that because snoek are indeterminate serial spawners, females on the west coast move inshore between spawning events, where their principal prey—*Sardinops sajax* and *Engraulis japonicus*—are more abundant.

Females spawning off the western Agulhas Bank do not appear to move inshore to feed between spawning events, according to near equal sex ratios and low inshore catch rates in winter–spring (region 5). Although line catches in region 4 were highest during the spawning season, which at first glance may appear to be contradictory, CPUE was an order of magnitude lower than in region 3 or region 5, indicating relatively low inshore abundance at that time of the year. High female mean stomach content mass (60.1 g) and the significantly higher proportion of females than males with food (shared only with the inshore feeding ground of the WC) suggest that the offshore WAB functions as both spawning and feeding ground during winter–spring. In addition, PBSs have revealed that clupeids—adult sardine and round herring—are more abundant near the shelf edge of the WAB in winter than along the WC (Coetzee[5]), and dietary comparison (this study) showed that clupeids indeed represent a larger component of the offshore diet

[5] Coetzee, J. 2000. Personnal commun. Pelagic Section, Marine & Coastal Management, Private Bag X2, Roggebaai, 8012, Cape Town.

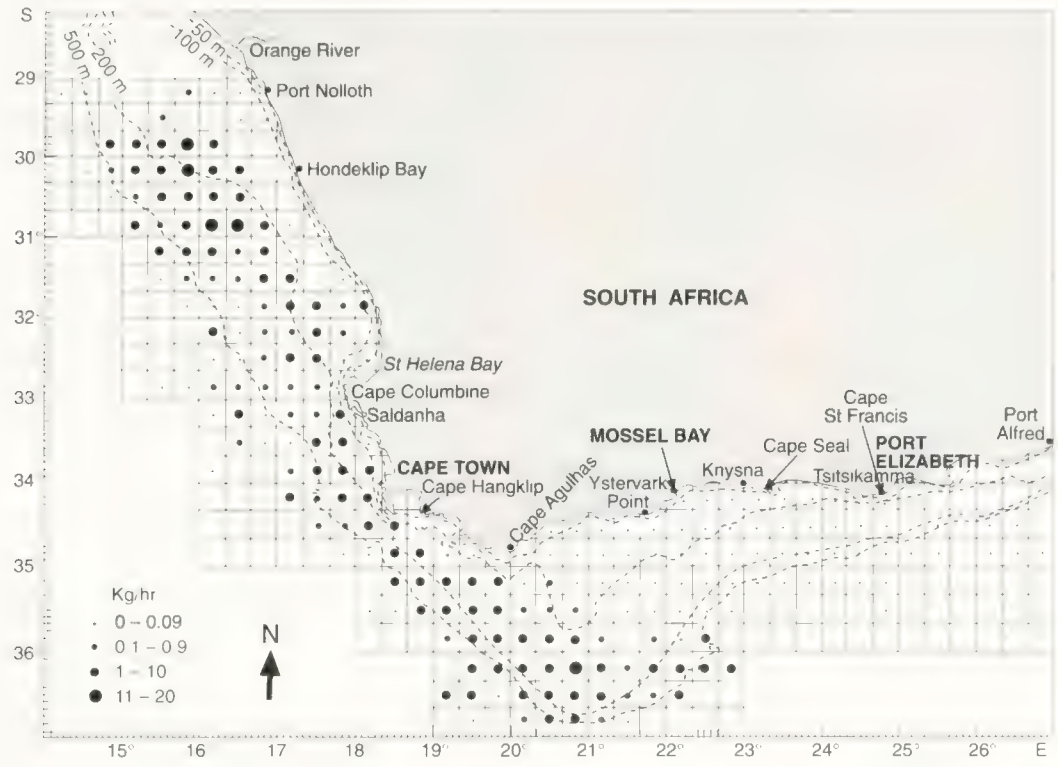

Figure 10

Catch per unit of effort (kg/h) by 20-mile block (1986–97) for *Thyrsites atun* caught by commercial trawls in the southern Benguela system during the spawning season.

of the WAB than offshore along the WC, where hake was dominant. Sex ratios and feeding patterns of adult snoek in the present study were confirmed as persistent biological features of the western Agulhas Bank by experimental trawl surveys on the spawning ground of region 4 during August 1999 and August 2000. The principal prey taxon for 1875 snoek with a sex ratio of 1M:1.2F ($P<0.001$) was Clupeidae (67% by weight); mean stomach content masses were 58.2 g for females and 27.6 g for males.

Even though young-of-the-year snoek were sampled (with fishing gear) in each of the seven regions, they formed a larger proportion (by mass and frequency of occurrence) of the diet of gannets at Bird Island (Lamberts Bay) than in gannets at Malgas Island. Either early juveniles are more abundant north of Cape Columbine than between Cape Columbine and Cape Infanta or they are selected at a higher frequency by gannets in the former area. Higher proportions of snoek smaller than 70 cm in the handline and pelagic-trawl catches of regions 0–2 than in catches from region 3 support the first suggestion, confirming that the area north of Cape Columbine has an important nursery function. Length frequencies of pelagically trawled, demersally trawled (<150 m), and line-caught snoek, nevertheless suggest a second nursery area to the east of Danger Point. But because handline catches in

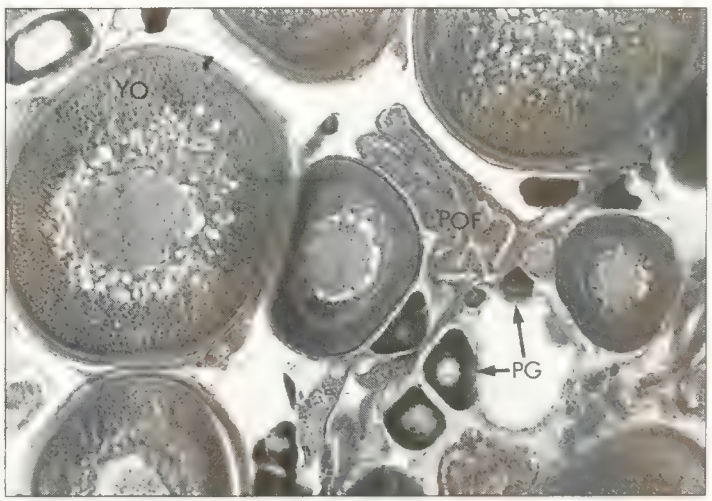

Figure 11

Photomicrograph of transverse section of *Thyrsites atun* ovary stained with haemotoxylin and eosin, showing co-occurrence of postovulatory follicles (POF) together with primary growth (PG) and advanced yolk-stage oocytes (YO).

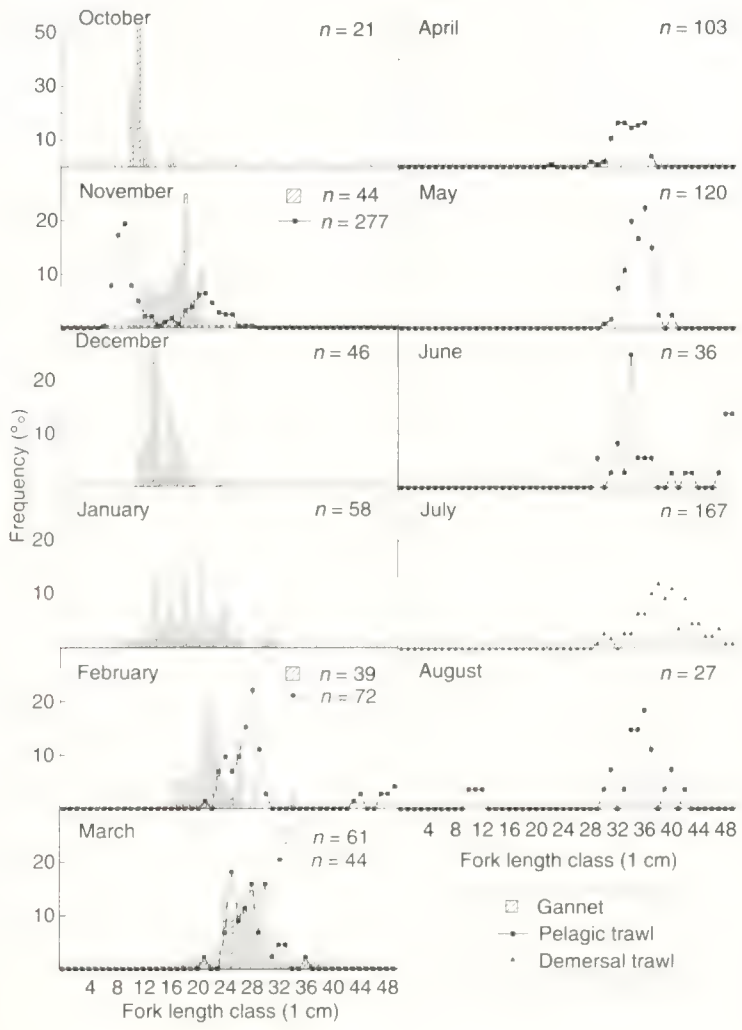

Figure 12

Monthly fork-length distributions of *Thyrsites atun* <50 cm caught by midwater trawls (1985–97), demersal trawls (1985–97), and Cape gannets (1978–97) in the southern Benguela system. *n* = sample size. Dotted line at 25 cm is included as a reference point.

regions 4 and 5 amounted to only 10% of those in regions 1and 2 (1985–97) and given that juvenile snoek made a substantially lower contribution to the diets of gannets foraging in this area, the area north of Cape Columbine is regarded as considerably more important to juvenile snoek. *Thyrsites atun* in demersal trawls made deeper than 150 m were mostly >65 cm, whereas those from shallower bottom trawls included substantial proportions smaller than this length. It is therefore concluded that the primary nursery ground is situated on the west coast, north of Cape Columbine and in water shallower than 150 m; a secondary nursery exists to the east of Danger Point. The absence of specimens <30 cm from demersal trawls, particularly those made shallower than 150 m, and their presence in pelagic trawls, indicates that 0-year-old snoek are largely epipelagic but become pelagic with growth (at ca. 8 months old).

The northward flowing Benguela Current provides a mechanism for transporting epipelagic snoek eggs and larvae (De Jager, 1955; Olivar and Fortuño, 1991) from the spawning ground to the proposed nursery areas. The Benguela current is found offshore (generally between the 150- and 400-m isobaths) and flows along the western edge of the Agulhas Bank and up the South African west coast; rate of flow is fastest (typically 25–80 cm/s) between Cape Point and Cape Columbine, where it develops into a shelf edge jet (Shannon and Nelson, 1996). Although water movement is primarily parallel to the shelf, inshore advection occurs to some degree due south of Danger Point and to a greater extent between Cape Columbine and Hon-

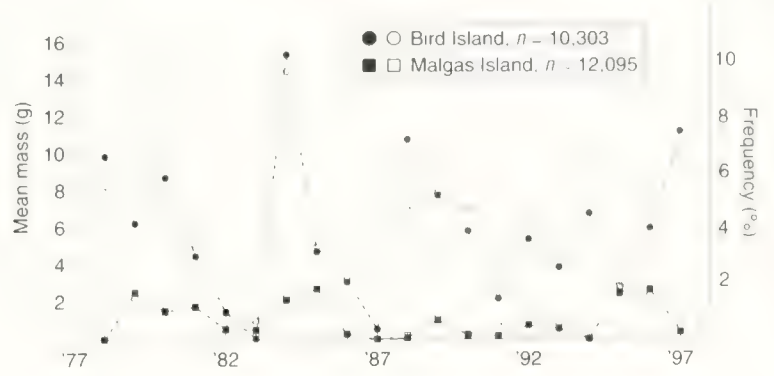

Figure 13

Annual frequency of occurrence (%*F*; dotted line) and mean mass (solid line) of *Thyrsites atun* in the stomachs of Cape gannets from Bird Island (circles) and Malgas Island (squares), 1978–97. *n*=number of gannet stomachs examined.

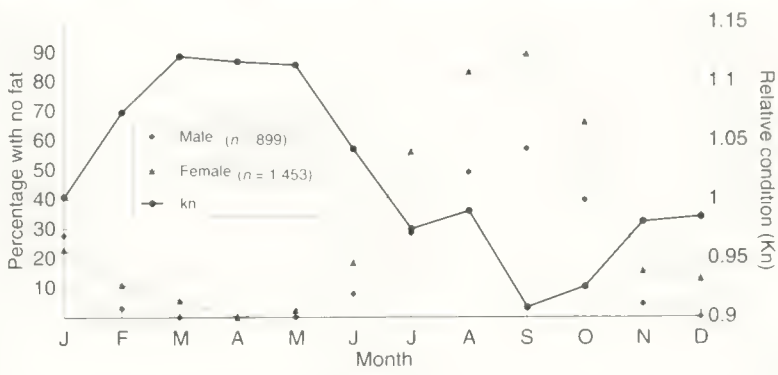

Figure 14

Mean monthly relative condition (Kn) and the proportion of adult *Thyrsites atun* (≥75 cm) without intestinal fat reserves, in the southern Benguela Ecosystem (1994–97).

deklip Bay (Shelton and Hutchings, 1990; Shannon and Nelson, 1996).

Snoek hatch about 2 days (50 hours) after fertilization (De Jager, 1955), are phytoplanktivorous from first feeding (3.5 mm and 3–4 days after hatching) until 8 mm long (standard length), after which they prey largely on the larvae of other fishes (Haigh, 1972). Total abundance of fish larvae in the southern Benguela is highest in spring and summer (Shelton, 1986); snoek larvae spawned during the winter and spring months are therefore assured of an abundant supply of food. Following northward advection in the jet current, young-of-the-year anchovy, round herring, and sardine, which share the northern nursery area with snoek, move shoreward across the shelf, with a concomitant increase in size (Armstrong et al., 1987; Roel and Armstrong 1991; Hampton, 1992; Roel et al., 1994; Barange et al., 1999; Van der Lingen and Merkle, 1999). They arrive at the coast from February through through June at total lengths of 5–11 cm, and, unlike snoek, which are found on the nursery grounds for 2–3 years, immediately begin a southwards migration back onto the Agulhas Bank, where they were originally spawned. Coupled with earlier spawning, rapid growth ensures that 0-year-old snoek are large enough (ca. 35 cm TL) to partake with the older juveniles in this seasonally abundant food source. Substantial increases in line catches during the period of clupeoid recruitment suggest that juvenile snoek follow their prey inshore. Differences in the size and age composition of catches north and south of Cape Columbine, however, indicate that they do not move southwards with them and onto the Agulhas Bank. The large contribution of lanternfish to the diets of snoek <50 cm is attributed to the fact that most of these fish were sampled during the second half of the year, i.e. when juvenile clupeoids (i.e.

Table 3

Stomach contents of snoek (*Thyrsites atun*) sampled inshore of the 150-m isobath along South African west coast (1994–97). *M* = percent mass, *F* = percent frequency of occurrence, *IRI* = percent index of relative prey importance at the species and at a higher (bold) taxonomic level. [P] = pelagic and [D] = demersal species.

Taxon and prey item	5–24 cm FL (n = 11)			25–49 cm FL (n = 212)			50–74 cm FL (n = 540)			>74 cm FL (n = 1,069)		
	M	*F*	*IRI*	*M*	*F*	*IRI*	*M*	*F*	*IRI*	*M*	*F*	*IRI*
Annelida							<0.1	0.2	**<0.1**	0	0	0
Polychaeta							<0.1	0.2	<0.1			
Crustacea	27.7	54.5	**24.7**	19.4	45.5	**12.6**	22.0	39.5	**14.3**	7.4	5.9	0.5
Amphipoda												
Themisto gaudichaudi[P]	20.9	9.1	14.2	17.8	42.0	32.4	1.42	10.9	1.0			
Brachyura												
Megalopa larvae[P]							<0.1	0.2	<0.1			
Euphausiacea												
Euphausia lucens[P]	6.8	45.5	23.0	1.3	3.6	0.2	15.0	27.4	26.0	0.3	1.6	<0.1
Isopoda												
Paridotea ungulata[P]							<0.1	<0.1	<0.1	<0.1	0.1	<0.1
Macrura												
Lobster pueruli[P]							<0.1	0.2	<0.1	<0.1	0.3	<0.1
Pasiphaea spp.[P]							<0.1	0.5	<0.1	0	0	0
Mysidacea[P]				<0.1	0.9	<0.1	0.3	1.0	<0.1	<0.1	0.1	<0.1
Stomatopoda												
Pterygosquilla armata[P]							5.0	10.4	3.3	7.1	4.5	1.1
Unidentified crustaceans				0.3	0.9	<0.1	0.1	0.6	<0.1	<0.1	0.3	<0.1
Mollusca												
Cephalopoda							0.3	2.2	**<0.1**	0.2	1.6	**<0.1**
Inioteuthis							<0.1	0.2	<0.1	0	0	0
Loligo vulgaris reynaudii							0	0	0	<0.1	0.3	<0.1
Lolliguncula mercatoris?							0.2	1.5	<0.1	<0.1	1.1	<0.1
Lycoteuthis?							0	0	0	<0.1	0.1	<0.1
Sepia australis							0.1	0.4	<0.1	<0.1	0.1	<0.1
Todaropsis eblanae							0	0	0	<0.1	0.1	<0.1
Unidentified squid							<0.1	0.2	<0.1	0	0	0
Teleostei	72.3	63.6	**75.3**	80.6	76.0	**87.4**	77.8	66.9	**85.7**	92.4	95.7	**99.5**
Engraulis japonicus[P]				6.1	10.7	2.8	30.9	19.6	38.3	26.9	44.0	38.6
Sardinops sagax[P]				8.9	6.3	2.4	18.9	6.8	11.7	43.1	33.8	47.4
Etrumeus whiteheadi[P]				5.1	1.8	0.4	6.5	3.2	1.3	2.3	3.5	0.3
Lampanyctodes hectoris[P]	68.4	9.1	46.5	37.2	21.4	34.4	0.8	1.9	0.1	0.4	1.3	<0.1
Maurolicus muelleri[P]				1.0	2.7	0.1	0.8	1.5	0.1	<0.1	<0.1	<0.1
Trachurus t. capensis[P]							4.1	2.4	0.6	3.9	6.8	0.9
Scomber japonicus[P]							0	0	0	0.5	0.1	<0.1
Lepidopus caudatus[P]							0.3	0.4	<0.1	0.1	0.5	<0.1
Thyrsites atun[P]							0	0	0	<0.1	0.1	<0.1
Sufflogobius bibartus[P]							1.3	1.0	0.1	0.1	0.2	<0.1
Gonorhynchus gonorhynchus							0	0	0	0.2	1.1	<0.1
Gnathophis capensis							<0.1	0.2	<0.1	0.3	2.9	<0.1
Merluccius spp.[D]				5.0	1.8	0.4	5.7	5.2	1.9	3.1	2.6	0.3
Clinidae[D]							<0.1	0.2	<0.1	<0.1	0.1	<0.1
Emmelichthys nitidus[D]							0	0	0	0.5	0.1	<0.1
Spondyliosoma emarginatum[D]							0	0	0	0.3	0.2	<0.1
Unidentified Teleostei	4	54.5	16.3	17.4	35.7	28.8	8.5	29.3	15.7	10.7	33.0	11.5

Table 4

Stomach contents of snoek (*Thyrsites atun*) sampled offshore of the 150-m isobath along the west coast (regions 1–3) and the western Agulhas Bank (regions 4 and 5) (1994–97). *M* = percent mass, *F* = percent frequency of occurrence, *IRI* = percent index of relative prey importance at the species and at a higher (bold) taxonomic levels. [P] = pelagic and [D] = demersal species.

	West coast						Western Agulhas Bank					
	50–74 cm FL (n = 147)			≥75 cm FL (n = 447)			50 – 74 cm FL (n =336)			≥75 cm FL (n = 367)		
Taxon and prey item	*M*	*F*	*IRI*	*M*	*F*	*IRI*	*M*	*F*	*IRI*	*M*	*F*	*IRI*
Annelida				<0.1	<0.1	**<0.1**						
Polychaeta				<0.1	<0.1	<0.1						
Crustacea	1.3	4.8	**0.1**	1.5	6.9	**0.1**						
Amphipoda												
Themisto gaudichaudi[P]				0.1	0.2	<0.1						
Brachyura												
Parapagurus dimorphus[D]	0.1	0.7	<0.1	0.1	0.4	<0.1						
Euphausiacea												
Euphausia lucens[P]	1.1	3.4	0.2	1.3	5.3	0.4						
Macrura												
Funchalia?[P]	<0.1	0.7	<0.1	<0.1	0.7	<0.1						
Stomatopoda												
Pterygosquilla armata[P]				0.1	0.4	<0.1						
Mollusca												
Cephalopoda				1.4	2.7	**<0.1**				1.7	1.9	**<0.1**
Lycoteuthis?				0.1	0.2	<0.1						
Sepia australis				0.1	0.4	<0.1						
Todaropsis eblanae				1.2	1.8	0.1				1.7	1.4	0.1
Unidentified squid				<0.1	0.2	<0.1				<0.1	0.5	<0.1
Teleostei	98.7	97.3	**99.9**	97.1	96.4	**99.8**	100	100	**100**	98.3	99.4	**99.9**
Engraulis japonicus[P]	0.1	0.7	<0.1	<0.1	0.2	<0.1	0.2	0.6	<0.1	0.1	0.3	<0.1
Sardinops sagax[P]	25.7	23.8	36.3	17.0	19.2	17.2	61.4	45.2	79.4	25.6	28.3	44.4
Etrumeus whiteheadi[P]	18.5	13.6	14.9	4.9	5.4	1.4	19.6	22.9	12.9	6.3	11.2	4.3
Lampanyctodes hectoris[P]	4.5	12.2	3.2	6.0	18.1	5.7				1.0	4.1	0.3
Maurolicus muelleri[P]	2.5	7.5	1.1	1.4	13.0	1.0	0.4	5.4	0.1	0.2	3.5	<0.1
Trachurus t. capensis[P]				13.2	12.8	8.8	1.4	0.6	<0.1	14.2	10.1	8.8
Scomber japonicus[P]	5.3	0.7	0.2							3.0	1.6	0.1
Lepidopus caudatus[P]	2.6	2.7	0.4	1.2	0.9	0.1				9.3	6.0	3.4
Thyrsites atun[P]										0.8	0.3	<0.1
Gonorhynchus gonorhynchus[D]							2.6	2.7	0.2	4.7	6.8	2.0
Emmelichthys nitidus[D]										<0.1	0.3	<0.1
Diaphus hudsoni[P]				<0.1	0.2	<0.1				<0.1	0.3	<0.1
Scomberesox saurus[P]							1.9	0.9	0.1	0.2	0.3	<0.1
Merluccius spp.[D 1]	31.4	15.0	27.8	47.6	24.4	60.8	4.4	3.3	0.4	28.0	18.5	31.8
Caelorinvhus simorhynchus[D]				0.1	0.7	<0.1						
Sebastes capensis[D]	0.5	0.7	<0.1	0.4	0.4	<0.1				0.2	0.5	<0.1
Zeus capensis[D]				0.7	0.2	<0.1						
Paracallionymus costatus[D]	0.6	0.7	<0.1	1.8	3.6	0.3				1.5	1.6	0.2
Unidentified Teleostei	6.9	37.4	15.2	2.8	24.8	3.7	8.1	30.4	7.0	3.2	23.4	4.6

[1] Two species of hake occur in South African waters—*M. paradoxus* and *M. capensis*–but owing to difficulty differentiating partially digested specimens, they were not analyzed separately.

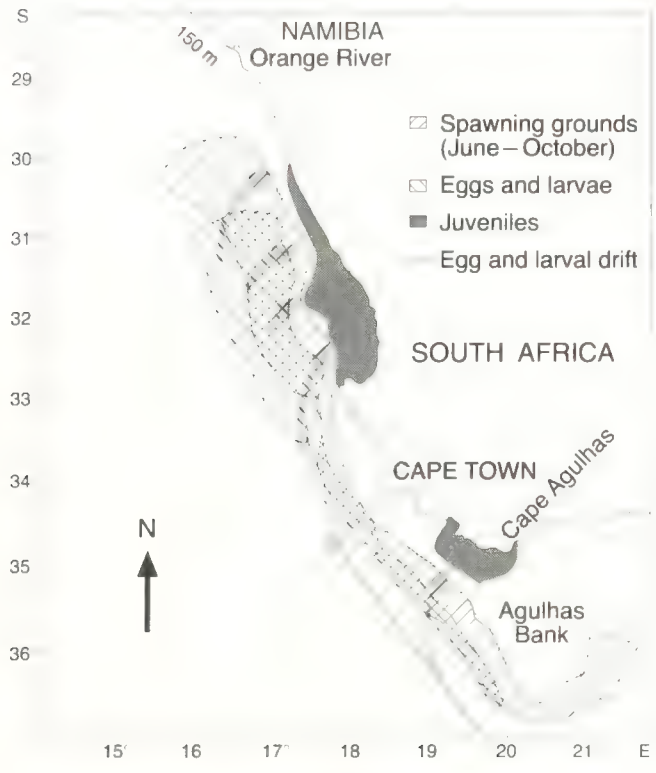

Figure 15

Conceptual model depicting the life history of *Thyrsites atun* in the southern Benguela ecosystem, including spawning grounds, distribution and transport of eggs and larvae, and the nursery areas.

Table 5

Proportions (%) of stomachs with food, and the mean mass of stomach contents for adult (>75 cm) male (M) and female (F) *T. atun* sampled on the South African west coast (WC; regions 1–3) and western Agulhas Bank (WAB; regions 4 and 5). χ^2 values were based on the frequencies of males and females with and without stomach contents (2×2 contingency tables) in each area (Yates' correction factor was applied as df =1). Significance levels are given by * (P<0.05), ** (P<0.01), and *** (P<0.001).

Area	Sex	n	%	χ^2	Mean mass (g)
Summer–autumn					
$WC_{inshore}$	M	197	50.2	0.18	13.3
	F	383	52.5		22.1
Winter–spring					
$WC_{inshore}$	M	130	52.4	6.6*	34.0
	F	729	81.2		43.0
$WC_{offshore}$	M	374	61.8	2.5	39.0
	F	193	69.0		44.6
$WAB_{combined}$	M	212	49.5	15.2**	38.4
	F	336	67		60.1

those small enough to be eaten by young snoek) are least abundant inshore.

Given that the majority of the alternative prey are most abundant at some distance from the coast—euphausids between 10 and 20 km from the coast (Pillar, 1986; Hutchings et al., 1991), lanternfish, and lightfish between the 75- and 300-m isobaths (Hulley and Prosch, 1987), and mantis shrimp in the 20–200 m depth zone (Griffiths and Blaine, 1988)—it is likely that juvenile snoek move farther offshore when anchovy recruits leave the area, i.e. beyond the normal operating range of line fishermen in regions 0–2 (hence the seasonal drop in handline CPUE).

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Abstract—The problem of bias in female petrale sole age and length-at-maturity relationships caused by sampling from spawning aggregations was investigated. Samples were collected prior to aggregation, and histological methods were used to determine maturity status. Mature and immature fish were classified by inspecting oocytes for the presence of yolk in September, when substantial divergence in yolked and unyolked oocyte diameters had been observed. Comparison of macroscopic and microscopic assessment of maturity showed that maturity status cannot be determined accurately by using macroscopic inspection during the summer. Female petrale sole from the central Oregon coast were 50% mature at 33 cm and 5 years of age. Comparison of data from our study with data used in recent petrale sole stock assessments showed that both sampling bias and the use of samples from seasons when status cannot be accurately determined have likely caused errors in fitted maturity relationships.

Length and age at maturity of female petrale sole (*Eopsetta jordani*) determined from samples collected prior to spawning aggregation

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Petrale sole (*Eopsetta jordani*) have been the target of a valuable commercial trawl fishery off the U.S. West Coast since before World War II (Sampson and Lee[1]). Management and assessment of petrale sole is complicated by the fact that modern fishing activity targets winter deepwater aggregations of spawning fish (Fig. 1). Because most of the available female maturity data are derived from the winter commercial fishery, they are potentially biased with respect to age and length at maturity (e.g. small mature fish are more likely to be sampled than small immature fish). Some summer samples are available for analysis, including those from the National Marine Fisheries Service triennial shelf survey (e.g. Zimmermann et al., 1994). However, in the summer, when mature and immature fish are well mixed, maturity status is not easily determined visually because of the similarity in appearance between ovaries of immature fish and those of fish in the "resting" state (Ketchen and Forrester, 1966).

The age and length at maturity for female fish is an important parameter in many stock assessment models. Clark (1991), Lunsford (1999) and Al-Jufaily (1996) have demonstrated that variation in the age at 50% maturity, especially in relation to the median age of recruitment to the fishery, can have a major influence on the calculation of a target fishing rate. Target fishing rates are currently used by the Pacific Fishery Management Council (PFMC) to manage most groundfish stocks (Clark, 1991; PFMC[2]). An example of a target fishing rate would be $F_{40\%}$, the fishing mortality rate that would reduce spawning stock biomass per recruit to 40% of the unexploited level. The potential influence of errors in estimating the median age of female maturity can perhaps best be illustrated with an example. In Lunsford's (1999) study of maturity of Pacific ocean perch

[1] Sampson, D. B., and Y. W. Lee. 1999. An assessment of the stocks of petrale sole off Washington, Oregon and Northern California in 1998. *In* Pacific Fishery Management Council. 1999. Appendix to the status of the Pacific coast groundfish fishery through 1999 and recommended acceptable catches for 2000: stock assessment and fishery evaluation. Pacific Fishery Management Council, 2130 SW Fifth Avenue, Suite 224, Portland, Oregon, 97201.

[2] Pacific Fishery Management Council. 2000. Status of the Pacific Coast groundfish fishery through 2000 and recommended biological catches for 2001: stock assessment and fishery evaluation. (Document prepared for the council and its advisory entities.) Pacific Fishery Management Council 2130 SW Fifth Avenue, Suite 224, Portland, Oregon 97201.

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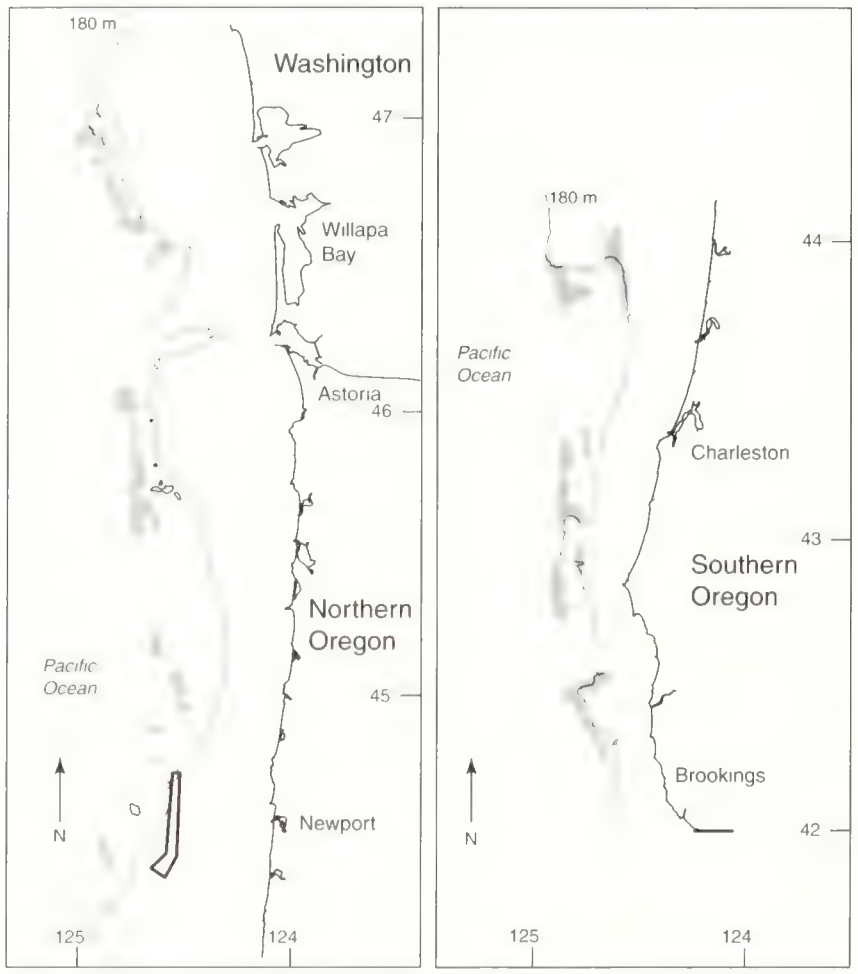

Figure 1

Sampling area for petrale sole (bold-outline polygon) off Newport, Oregon, and areas where winter trawl fishing for petrale sole is concentrated (gray polygons). Also shown is the 180-m depth contour.

(*Sebastes alutus*), a shift in the estimated median age of maturity for female fish from 7.5 to 10.5 years decreased the $F_{40\%}$ value from 0.110 to 0.076, a decrease of 31%. Accordingly, the use of potentially biased maturity data from the winter commercial fishery for petrale sole adds to the uncertainty in stock assessments. The accuracy of maturity information used in recent petrale sole stock assessments is also uncertain because of two additional factors: outmoded data and the blending of samples across space and time (Sampson and Lee.[1]; Turnock et al.[3]). Maturity samples are obtained from various locations and times, and are often combined to produce a general relationship for stock assessment purposes. The combined relationship may poorly account for geographical differences, long-term changes in maturity, or for inadequacies in some samples (e.g. lack of immature fish) (Sampson and Al-Jufaily, 1999) and can result in poorly determined curves that bias and degrade the fit of the combined maturity relationship. The principal objective of our study was to collect maturity data for female petrale sole from the late summer to early fall period and compare them with the maturity data used in recent stock assessments (Sampson and Lee[1]; Turnock et al.[3]). Although sampling in late summer and early fall is probably optimal for assessing female maturity in the petrale sole population, some ovaries may be difficult to classify accurately as mature or immature by macroscopic inspection. A second objective of our study was to evaluate female petrale sole maturity by using microscopic examination of stained thin sections and compare these results with those obtained from simple visual inspection.

The petrale sole maturity data used in recent stock assessments have been obtained from the Oregon Department of Fish and Wildlife's commercial fishery sampling program (Sampson and Lee[1]; Turnock et al.[3]). Potential

[3] Turnock, J., M. Wilkins, M. Saelens, and C. Wood. 1993. Status of West Coast petrale sole in 1993. Appendix G. *In* Status of the Pacific Coast groundfish fishery through 1993 and recommended biological catches for 1994: stock assessment and fishery evaluation. Pacific Fishery Managemenmt Council, 2130 SW Fifth Ave., Suite 224, Portland, OR 97201.

bias in some of these data, arising from spawning aggregation, argues that a different sampling approach might be useful for trying to generate unbiased maturity data from samples of the commercial catch. A third objective of our study was to evaluate problems with available maturity data from fishery samples in light of histological evaluations of maturity stages and to recommend an alternative approach for sampling the commercial catch for age and length at maturity.

Materials and methods

Petrale sole were collected by trawl during August and September 2000 by using a chartered commercial fishing vessel from Newport, Oregon. Sampling was conducted over a very limited geographic range to minimize any spatial variation in the maturity ogive. Individual sampling sites were selected to attempt to sample across the available size range of petrale sole, based on the skipper's experience and expertise. Fish were sorted at-sea according to total length (±0.5 cm), and fifteen fish from each 1-cm size interval were retained for maturity sampling. Upon returning to port, the fish were measured again and sex was determined by dissection. An ovary was removed and assigned a macroscopic maturity stage following the criteria of Hagerman (1952). Only experienced samplers were used to assign macroscopic maturity stages to minimize any errors in visual staging. Otoliths were removed from all female fish for subsequent age determination, and one ovary was preserved for histological examination to determine maturity. Ages were determined by using the break-and-burn technique for sagittal otoliths (Chilton and Beamish, 1982). Consistency of age determination was evaluated by using a blind double reading.

Ovaries were preserved in 10% buffered formalin and later transferred to 70% ethanol for storage. Tissue samples from the midsection of the ovary were then embedded in paraffin, sectioned at 5 µm, and stained with Harris's hematoxylin and eosin Y. The samples were examined and classified as mature or immature based on the presence or absence of dark-staining yolk globules (vitellogenin).

The diameter (µm) of the largest spherical nonatretic oocyte in the most advanced oocyte stage from each of five microscope fields was also measured and used to calculate a mean maximum oocyte diameter (MMOD) for each sectioned ovary (West, 1990; Nichol and Pikitch, 1994). MMOD was compared for mature and immature fish. A divergence in MMOD between mature and immature fish was taken as evidence that the presence or absence of dark-staining yolk globules was an accurate indicator of maturity status. Samples from August and September were compared by using this approach. The accuracy of visual examination of ovaries was then evaluated by comparing the maturity status from visual examination with status determined after sectioning, staining, and microscopic examination.

Logistic regression was used to fit sigmoid length-maturity and age-maturity curves. The model fitted had the general form

$$P_{x_1} = e^{(b_0 + b_1 x_1)} / (1 + e^{(b_0 + b_1 x_1)}),$$

where p = the probability that a fish is mature in a given length (cm) or age category x_1; and
b_0 and b_1 are parameters that define the shape and location of the fitted curve.

The predicted length or age at 50% maturity was calculated as

$$L \text{ (or } A)_{50} = -b_0/b_1.$$

Maturity data collected by the Oregon Department of Fish and Wildlife (ODFW) from the 1986–2000 commercial trawl fisheries were also analyzed and compared with the data collected in our study. The most recent petrale sole stock assessment (Sampson and Lee[1]) relied on maturity data used for the 1993 assessment (Turnock et al.[3]), which in turn were derived from combined ODFW port sampling data for the years 1986–91. We fitted a maturity-length relationship to these data for comparison with the maturity data from our study.

We also summarized the ODFW data from 1986–91 and 1992–2000, by month and maturity status, to compare with our data and assess their adequacy for determining length at maturity for female petrale sole. All of these samples were classified by a simple visual evaluation of maturity stage. To examine the effect that a lack of immature fish may have had on estimated maturity curves from these two time periods, we split the data into groups, according to season. Samples from the months of November through February were classified as "fall–winter" samples. These samples represented the seasonal time period when the maturity status of petrale sole was most readily determined visually, but also the time period when samples were most likely to be from spawning aggregations. Samples from April through September were classified as "spring–summer" and represented the seasons in which fish were not aggregated for spawning, but the time when maturity status was most difficult to determine by inspection of the ovaries.

Results

Comparison of visual maturity determinations with results obtained from microscopic evaluation showed that maturity of petrale sole cannot be reliably determined by simple visual inspection in August or September (Tables 1 and 2). For ovaries classified as immature by inspection in August, 16.7% proved to be mature upon microscopic evaluation. Of those classified initially as mature, 6.5% showed no microscopic evidence of vitellogenesis. By September, all of the ovaries classified by inspection as mature, did prove to be vitellogenic. However, 27.9% of those classified as immature, proved to be vitellogenic after viewing the stained sections with a microscope.

MMOD increased markedly in vitellogenic ovaries between August and September, but in nonvitellogenic ovaries the increase was minimal (Fig. 2). The resulting divergence in MMOD and the absence of fish with MMOD

Table 1

Details of petrale sole collected by trawl aboard the FV *Olympic*.

Date	Location	Females	Males	Size range (cm)
8 Aug 2000	4428°N 12434°W	140	103	24–51
23 Aug 2000	4446°N 12432°W	24	46	27–49
26 Sep 2000	4428°N 12435°W	117	123	26–50
Total		281	272	24–51

Table 2

Comparison of macroscopic and microscopic determination of maturity in female petrale sole collected by trawl.

	Macroscopic classification		Microscopic classification	
Sample month	Condition	Number of fish	Number immature (%)	Number mature (%)
August	immature	102	85 (83.3)	17 (16.7)
	mature	62	4 (6.5)	58 (93.5)
September	immature	61	44 (72.1)	17 (27.9)
	mature	56	0 (0.0)	56 (100)
Total		281		

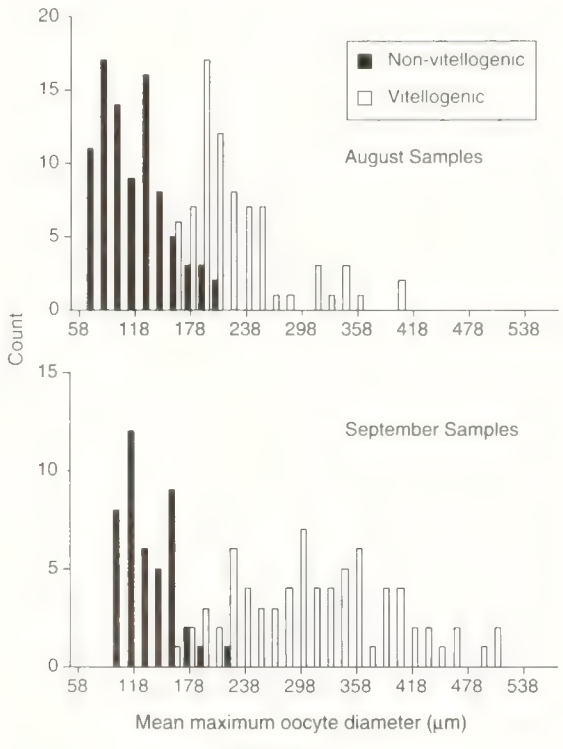

Figure 2

Comparison of mean maximum oocyte diameters (µm, see text) for petrale sole with vitellogenic and nonvitellogenic oocytes, for samples collected in August and September 2000.

around 180 µm suggested that by September, the microscopic classification of ovaries provided an accurate identification of maturity status of individual fish. Immature fish were well represented in the September collections, indicating the fish were still well mixed on the feeding grounds (Table 2). Therefore, the September maturity data generated from microscopic inspection were used to fit age- and length-at-maturity relationships for female petrale sole (Fig. 3). The resulting curves fitted the data well and chi-square tests on the residuals indicated no problems with lack of fit caused by overdispersion (Pearson chi-square of 5.714 [with 20 degrees of freedom] for length, and 0.643 [with 11 degrees of freedom] for age, $P>0.999$). The fitted relationships indicated that female petrale sole off the central Oregon coast were 50% mature at about 33 cm and at about 5 years of age. Complete maturity was obtained at about 40 cm and about 9 years of age (Table 3).

Examination of the monthly samples that, as an aggregate, were used to fit the 1986–91 maturity curve showed that numerous samples were included from the March through August period, especially from the port of Charleston, Oregon (Table 4). The inclusion of these summer samples explains some of the flatness in the fitted maturity curve from Turnock et al.[3] (Fig. 4, L_{50}=30.6, slope=0.29). A maturity curve fitted to these data, but excluding spring and summer samples, was much steeper (Fig. 4, L_{50}=33.56, slope=0.50).

Inspection of the 1986–91 and 1992–2000 maturity data from the winter months, when errors in determining maturity should be minimized (Tables 4 and 5, Fig. 5), showed some evidence of the type of bias that can result from sampling spawning aggregations. First, very few im-

Table 3

Results of logistic regression analysis of histologically determined maturity status of petrale sole versus length (cm) and age (September samples only).

Independent variable		Coefficients	Standard error	Chi-square	*P*-value	L_{50} or A_{50}	95% confidence
Length						33.10 cm	32.13–33.93
	constant	−24.593	4.572	28.936	0.0001		
	length	0.743	0.136	29.759	0.0001		
Age						5.15 yr	4.68–5.54
	constant	−6.358	1.417	20.122	0.0001		
	age	1.234	0.261	22.349	0.0001		

mature fish were sampled, even though the commercial fishery samples showed a similar lower size range to the fish collected in our study (Fig. 6). The lack of immature fish was most evident in the 1986–91 November–February samples from Charleston, Oregon, where 170 fish were sampled for maturity, and only one fish was reported as immature. The 1992–2000 Charleston data also showed low numbers of immature fish. These samples also showed groups of very small fish, and most or all of them were classified as mature (Fig. 5). This kind of bias, where small fish encountered are more likely to be reported as mature than similar-size fish sampled from a well-mixed population, would also act to flatten the resultant maturity curve. The Astoria winter data included more immature fish, and accordingly produced steeper maturity curves. However it was unclear to what degree bias from sampling spawning aggregations may have influenced these curves.

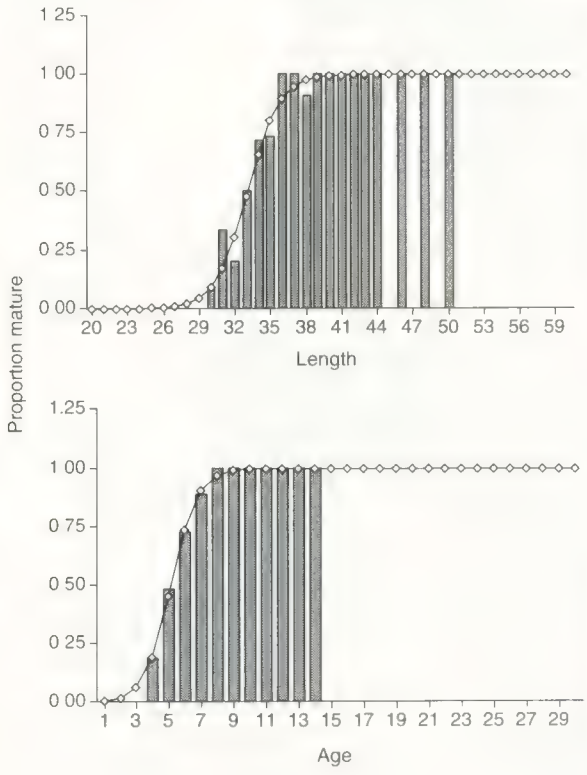

Figure 3

Proportion mature for female petrale sole, by age and length (FL,cm), from September samples. Maturity status was determined by histological examination by using presence and absence of vitellogenesis to determine maturity. Fitted curve is also shown (Table 3).

Discussion

Although it is known that late fall and winter is a better time for visually assessing female maturity status for petrale sole, our data showed clearly that late summer and early fall maturity samples, for which there was a visual determination of maturity, should not be used for estimating maturity in this species. Although our study did not specifically examine ovaries from spring collections, the general timing of ovarian development in this species suggests that this caution can be extended to all late spring and summer samples. Our results are similar to the findings of Ramsay and Witthames (1996), who suggested that visual maturity evaluations of the common sole (*Solea solea*) are generally only reliable during a limited portion of the year.

The maturity data developed in our study (Figs. 3 and 4) suggest a larger size at 50% maturity (33.1 cm vs. 30.7 cm) and a much steeper maturity curve for petrale sole than indicated by the 1986–91 sample data used in the last two petrale sole stock assessments (Turnock et al.[3]). Although the curves appeared to be quite different, the length at 50% maturity increased by only 2.4 cm. The most recent stock assessment model indicates an annual fishing mortality rate, for fully exploited size groups, of 0.285 (Sampson and Lee[1]). Incorporating a revised maturity ogive from our study decreased the equilibrium fishing rate to 0.268, a change of about 6% (Sampson[4]). This modest effect on harvest rate seems odd, given the large apparent difference between the curves in Figure 3. A possible explanation for this discrepancy is that the results depend heav-

[4] Sampson, D. B. 2000. Personal commun. Coastal Oregon Marine Experiment Station and Department of Fisheries and Wildlife, Oregon State University, Hatfield Marine Science Center, Newport, OR 97365.

Table 4

Summary of the numbers of mature and immature petrale sole sampled, from the Oregon bottom trawl fishery, 1986–91.

Port	Month	Immature	Mature	Total
Astoria	November	20	130	150
Astoria	December	0	167	167
Astoria	January	2	135	137
Astoria	February	32	10	42
Winter total		54	442	496
Astoria	March	18	61	79
Astoria	October	7	26	33
Astoria total		79	529	608
Charleston	November	0	37	37
Charleston	December	1	68	69
Charleston	January	0	24	24
Charleston	February	0	40	40
Winter total		1	169	170
Charleston	March	16	64	80
Charleston	April	0	37	37
Charleston	June	14	115	129
Charleston	July	27	123	150
Charleston	August	71	162	233
Charleston	October	2	78	80
Charleston total		131	748	879
Total (all ports)		210	1277	1487

Table 5

Summary of numbers of mature and immature petrale sole sampled by season and port from the Oregon bottom trawl fishery, 1992–2000.

Port	Season	Immature	Mature	Total
Astoria	Winter (Nov–Feb)	19	242	261
	Spring–fall (Mar–Oct)	4	89	93
Charleston	Winter (Nov–Feb)	20	347	367
	Spring–fall (Mar–Oct)	31	179	210
Brookings	Winter (Nov–Feb)	0	56	56
	Spring–fall (Mar–Oct)	0	142	142
Total		84	995	1079

ily on assumptions about fishery selectivity and discard used in the latest assessment model–parameters that are poorly known for most West Coast fish stocks. The modest effect on harvest rate found in our study also does not preclude larger effects for other, later maturing stocks. In the example given earlier from Lunsford's (1999) simulation work with Pacific ocean perch, the drop in target harvest rate was much larger. In that instance, a shift of 3 years in the median age of female maturity resulted in a 31% drop in the target harvest rate. In that example, spawning stock biomass per recruit also fell to 31%, well under the target of $F_{40\%}$.

The maturity data developed in our study differ from those developed by Turnock et al.[3] primarily in the steepness of the maturity curve. It could be argued that the earlier curve is flatter simply because it incorporates data from a wider geographic range. A latitudinal cline in length at 50% maturity, as has been postulated for many flatfish stocks (Ketchen and Forrester, 1966; Castillo, 1995; Brodziak and Mikus, 2000), could cause flattening

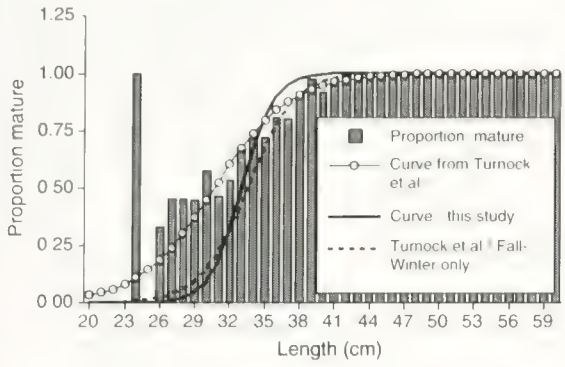

Figure 4

Comparison of fitted petrale sole female maturity curves from September samples (our study) and 1986–91 commercial fishery data used in the last two stock assessments (Turnock et al.[3]). Bars show 1986–91 maturity data used to fit the curve from Turnock et al.[3] Dashed line shows the maturity curve fitted to the 1986–91 samples by using only data from the fall–winter period.

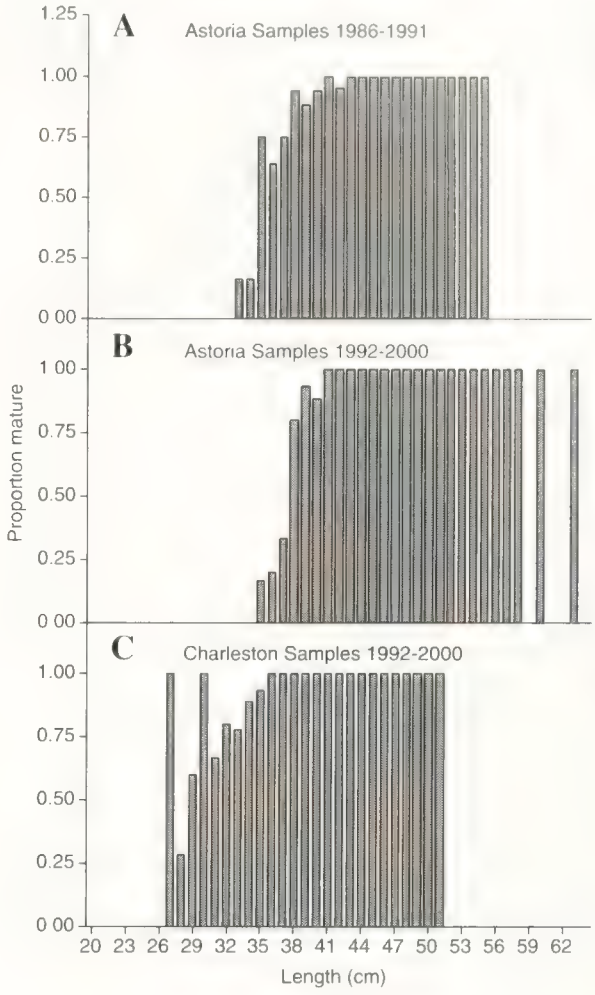

Figure 5

Proportion of female petrale sole identified as mature from November–February samples of trawl landings in Astoria and Charleston, Oregon, 1986–1991 and 1992–2000.

in a combined maturity curve. However, errors in determining maturity status, caused by including samples from time periods when maturity status cannot be accurately assessed visually, would have the same effect. This can be seen in a comparison of the maturity data generated in our study from macroscopic and microscopic evaluations. The macroscopic curve (bars and solid line in Figure 7) is flattened in relation to the curve according to microscopic evaluation (dashed line). The curve is also shifted to the right because, in this case, more large fish were incorrectly classified than small fish. At other times of the year, errors could be more common with smaller fish and the curve would shift the other way. In either case, however, the curve should, in theory, be flatter than the true maturity curve. This flattening of the maturity curve is caused by the way the most likely errors change along a maturity ogive. In small or young fish, which are mostly immature, most of the errors encountered will be immature fish mistakenly considered mature. At larger sizes or older ages, the reverse will be true. Near the inflection point, the two types of errors offset each other and have little impact on the slope because the population is split roughly 50/50 with respect to maturity. These effects, in combination, tend to flatten the resulting curve.

Compared to a length at 50% maturity of 33 cm for the central Oregon coast (our study), the Astoria data from the commercial fishery are consistent with an increase in the length at 50% maturity with latitude, as suggested by Ketchen and Forrester (1966) and Castillo (1995). The methods developed in our study could be applied to petrale sole samples collected over a wider geographic range to shed more light on how length at maturity varies with latitude. Best (1961) reported a length at 50% maturity of 35.5 cm for female petrale sole from California waters, and Harry[5] reported 40.0 cm for the Columbia River area. In comparison with the recent data from Astoria fishery samples (Fig. 5) and from the central Oregon coast (Fig. 3), the data from Harry[5] suggest a very large decrease in the length at 50% maturity for female petrale sole since the 1960s. If this decrease is a biological reponse to exploitation, it could explain how petrale sole stocks have held up quite well under heavy commercial harvest (Sampson and Lee[1]).

The data presented in our study suggest that the collection of maturity data by sampling on spawning aggregations does cause bias in estimates of female age and length at maturity for petrale sole. Use of spring and summer maturity samples in data sets used to estimate age and length at maturity has also caused errors. Our analysis shows that the overall effect on estimates of age and length

[5] Harry, G. Y. 1959. Time of spawning, length at maturity, and fecundity of the English, petrale and Dover soles (*Parophrys vetulus*, *Eopsetta jordani*, and *Microstomus pacificus*, respectively). Fish. Comm. Oregon, Research Briefs 7(1):5–13.

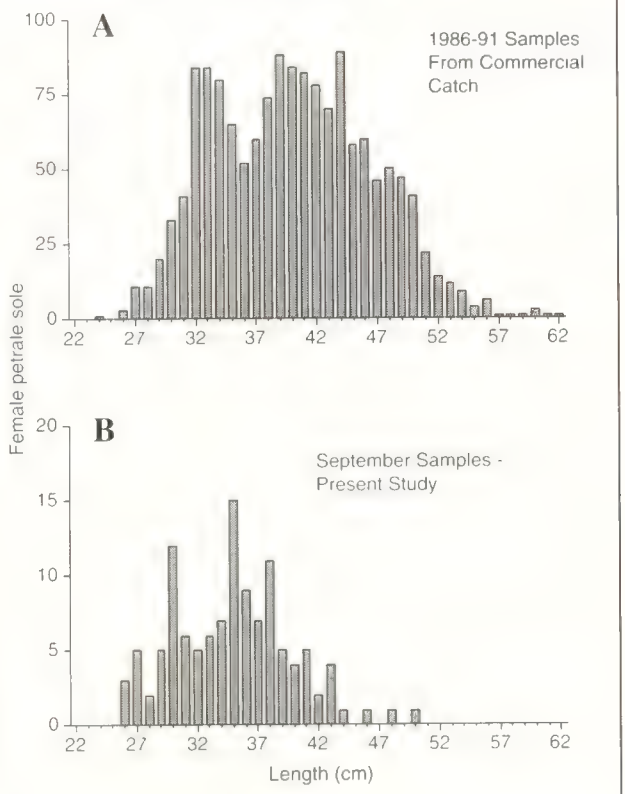

Figure 6

Comparison of female petrale sole length frequency from the 1986–91 commercial fishery samples and the September samples collected in our study. The 1986–91 samples were also used to fit the maturity curve from Turnock et al.[3]

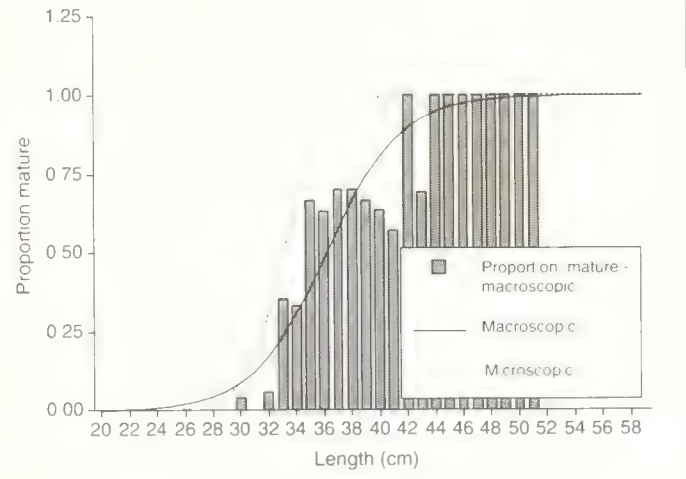

Figure 7

Comparison of maturity curves fitted to the data from our study. Bars show proportion of fish mature by length from the macroscopic evaluations of the August and September samples. The solid line is the fitted curve for those data. The dashed line is the fitted curve from microscopic evaluations of the September samples only.

at 50% maturity has been small. Collection of early fall samples from the commercial catch, followed by histological preparation and classification based on presence or absence of vitellogenin, should yield more accurate maturity information for female petrale sole than winter sampling on spawning aggregations or maturity sampling where only a visual assessment of ovary condition is made.

Acknowledgments

We'd like to thank the skipper and crew of the FV *Olympic*. Staff from ODFW's Marine Program and from the Pacific States Marine Fisheries Commission helped with sample preparation. Jennifer Menkel aged the otoliths and Margo Whipple of Oregon State University prepared the histological sections. Jim Golden and David Sampson provided helpful reviews of the draft manuscript.

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The measurement error in marine survey catches: the bottom trawl case

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Abstract—We have formulated a model for analyzing the measurement error in marine survey abundance estimates by using data from parallel surveys (trawl haul or acoustic measurement). The measurement error is defined as the component of the variability that cannot be explained by covariates such as temperature, depth, bottom type, etc. The method presented is general, but we concentrate on bottom trawl catches of cod (*Gadus morhua*). Catches of cod from 10 parallel trawling experiments in the Barents Sea with a total of 130 paired hauls were used to estimate the measurement error in trawl hauls. Based on the experimental data, the measurement error is fairly constant in size on the logarithmic scale and is independent of location, time, and fish density. Compared with the total variability of the winter and autumn surveys in the Barents Sea, the measurement error is small (approximately 2–5%, on the log scale, in terms of variance of catch per towed distance). Thus, the cod catch rate is a fairly precise measure of fish density at a given site at a given time.

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Surveys are vital for estimating the size and composition of marine populations. In the data collection process, trawl samples or acoustics (or both) are usually employed. It is well known that the resulting estimates are subject to substantial variations, and it is important to quantify and explain, as much as is possible, the variability in terms of relevant explanatory variables or covariates. Typically these variables will depend on the sampling tool used, but for bottom trawl catches important explanatory variables can be depth and location of the haul (Polacheck and Vølstad, 1993), time of the day (Korsbrekke and Nakken, 1999), season, strength of the year classes involved, etc.

Generally, as the number of covariates increases, and the model becomes more complex, the residual variation (or remaining uncertainty) not explained by the model decreases. But no matter how refined the model is, there will always be an unexplained random component that cannot be attributed to any observed variable. This residual variation is caused by the interactions between the fish, the measurement device, and the environment (see e.g. Engås, 1994).

The purpose of this study was to define and quantify this residual source of random variation. This was done by analyzing measurements from parallel tows of multiple vessels, which is the closest one can come to a controlled statistical experiment in this context. The importance of quantifying this type of fluctuation lies in the fact that it is a benchmark uncertainty, which is inherent in the survey process itself, and in this sense it may be termed a measurement error. If the measurement error can be assessed from field data and is consistent over time and space, we improve our understanding and quantification of other causal factors behind the uncertainty associated with survey estimates.

In this study we looked at bottom trawl catches of cod, but we would like to stress that the concepts and techniques developed can in principle be applied to acoustic survey estimates or indeed to any type of measurements collected simultaneously by two or more independent parallel sampling devices. It should be noted that there is a growing related literature on comparative survey analysis. We refer to the review paper by Pelletier (1998) and references therein.

Materials and methods

Parallel trawling experiments

During the annual combined bottom trawl and acoustic survey of demersal fish in the Barents Sea during winter and autumn conducted by the Institute

Table 1

Summary statistics for the parallel trawling experiments; time, vessel, position (latitude, longitude), the number of hauls (n) and the average per cod weight w (in kg) within each group. The vessels involved were *Johan Hjort* (JH), *Anny Kræmer* (LIZY), *G. O. Sars* (GS), *Jan Mayen* (JM), and *Michael Sars* (MS).

Group	Year	Date	Vessels	Lat.	Long.	n	w
1	1991	3–5 Mar	LIZY, JH	71.3	26.2	10	2.01
2	1994	10 Feb	LIZY, JH	71.2	36.0	5	0.81
3	1994	22–23 Feb	LIZY, GS	71.3	26.3	8	1.98
4	1995	22–23 Feb	JM, JH	71.3	25.4	12	1.05
5	1995	23–25 Feb	JH, GS	71.3	25.4	23	0.94
6	1995	15–17 Aug	MS, JH	74.3	17.3	29	0.72
7	1996	17 Feb	JM, GS	70.4	36.5	4	0.03
8	1996	24–25 Feb	JM, GS	71.8	23.8	10	0.19
9	1997	8–10 Feb	JH, GS	71.3	27	17	0.72
10	1997	2–3 Aug	MS, JH	72–73	27–30	12	0.21

of Marine Research, Bergen (IMR), (Jakobsen et al.[1]), parallel trawling experiments were used to compare the efficiency of the participating vessels with gear types as given in Table 1 and Figure 1. During a parallel haul the vessels operated about 500 meters apart and used radio contact to assure proper coordination during hauls. We analyzed ten parallel trawl experiments performed by the IMR during the last decade (Table 1). The data from 1991 are described in Michalsen et al. (1996). Two hauls with unstable bottom contact were excluded from the 1991 data (Michalsen et al., 1996). Similarly, two hauls from 1995 were excluded—one where trawl geometry measurements indicated problems with the doors and another with highly different recorded towed distances (0.7 and 2.2 nautical miles [nmi]). Let $d_{i;j}$ denote the towed distance for haul i and vessel j; i=1, ... , n; j=1,2 where n is the total number of hauls. The average recorded distance is $\bar{d} = (2n)^{-1} \sum_{i=1}^{n} \sum_{j=1}^{2} d_{i;j} = 1.33$ nautical mile (average duration in time is 27 minutes), with $0.8 \le d_{i;j} \le 1.8$ in 98% of the cases. The absolute values $|d_{i;1} - d_{i;2}|$ of the differences in towed distance for the two vessels in the same haul, are 0, 0.1, 0.2, 0.3, 0.4, and 0.6 in 43, 45, 31, 6, 4, and 1 cases, respectively.

The data were subdivided into 10 groups so that the same two vessels performed all hauls within a group, within a period of one to three days, and usually in a small geographical area. Group 10 is an exception where the trawl stations are evenly spread over about 60 nmi both in the east–west and in the north–south directions.

The statistical model

Any study of uncertainty depends on the stochastic model adopted. Two different statistical models may yield quite different uncertainty estimates. A general model for a series of survey measurements $\{y_i, i=1, \dots, n\}$ is given by

$$y_i = f(x_{i1}, \dots, x_{ip}) + \varepsilon_i, \qquad i = 1, \dots, n,$$

where f = a deterministic function, which in general is unknown; and

$x_{i1}, \dots, x_{ip}$ = the ith measurements of p explanatory variables, such as geographical location, depth, or time.

If all of the relevant explanatory variables were included, ε_i would represent the residual uncertainty. In practice, all conceivable explanatory factors will not be observed, and often f is assumed to be linear.

A difficulty in assessing the uncertainty of fish abundance estimates is that we cannot carry out a controlled experiment, where the setting of each experiment is identical. In such an idealized series of experiments the explanatory variables $x_{i1}, \dots, x_{ip}$ would be fixed, and ε would be the only source of random variation so that for a series of N experiments,

$$y_k = f(x_1, \dots, x_p) + \varepsilon_k, \qquad k = 1, \dots, N.$$

The standard error of ε_k could then be estimated directly from the observations $\{y_k\}$ as

$$\hat{\sigma}_\varepsilon = \left[\frac{1}{N-1} \sum_{k=1}^{N} (y_k - \bar{y})^2 \right]^{\frac{1}{2}}.$$

and the correctness of the model could be tested by a new series of experiments for a new set of fixed values for the explanatory variables.

The closest we can come to such an idealized experiment is that of parallel trawling described above. The values of the explanatory variables, such as geographical location and depth, will vary somewhat from one vessel to another,

[1] Jakobsen, T., K. Korsbrekke, S. Mehl, and O. Nakken. 1997. Norwegian combined acoustic and bottom trawl surveys for demersal fish in the Barents Sea during winter. ICES CM 1997/Y:17:1–26. Institute of Marine Research, P.O.Box 1870 Nordnes, 5817 Bergen, Norway.

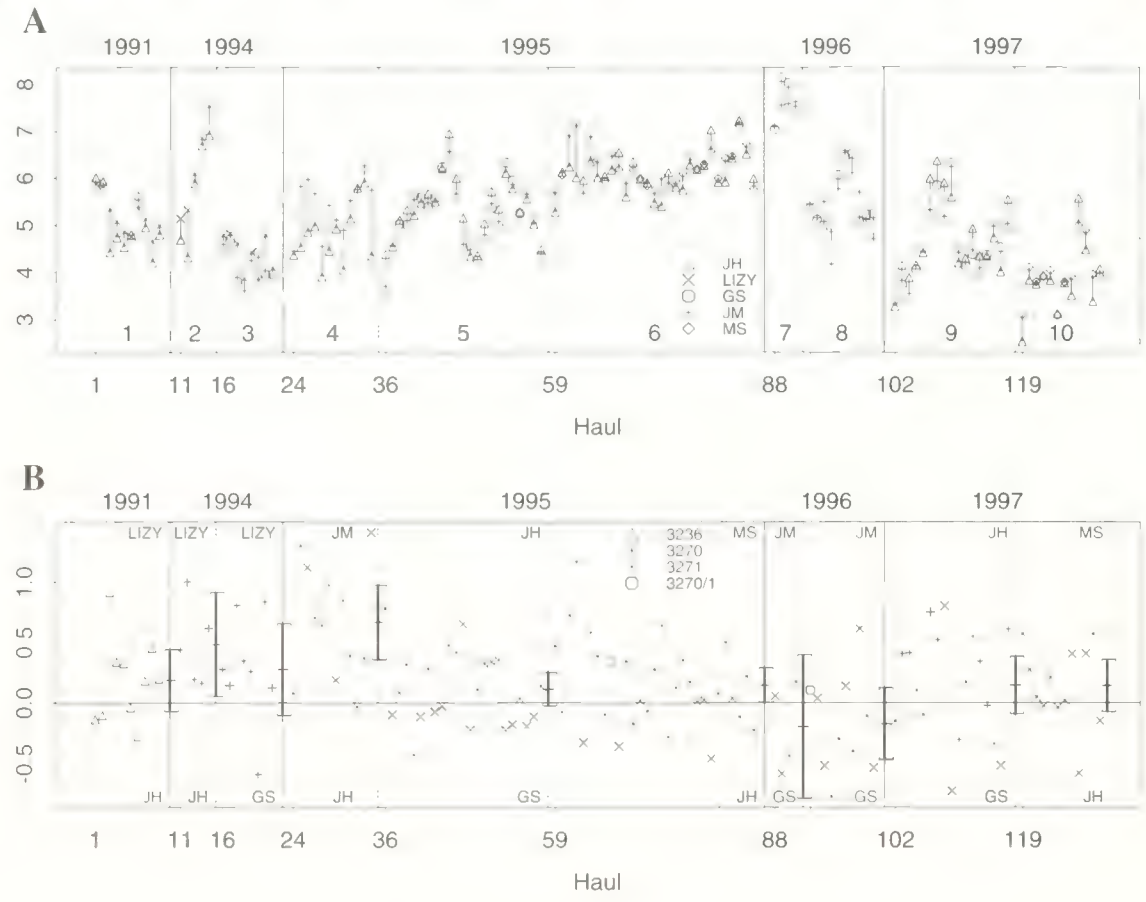

Figure 1

(**A**) Catches $y_{i,j}$ from the parallel trawling experiments in Table 1. The groups are separated by vertical lines and the group numbers corresponding to Table 1 are given at the bottom of the figure. The symbols represent vessels (see Table 1), and the cumulative number of hauls are given at the horizontal axis. (**B**) Corresponding differences $z_i = y_{i,1} - y_{i,2}$. The symbols indicate gear type; 3236: Campelen 1800 shrimp trawl with 35-mm mesh size, 40 m sweeps and rockhopper gear; 3270: same as 3236, but 20-mm mesh size; 3271: same as 3270 but with strapping. 3270/1 indicate that one vessel uses 3270, the other 3271. To the right, 95% confidence intervals for the group means are given. The first and second vessel in each group are given at the top and bottom, respectively, for each group.

but as an approximation they will be considered identical. However, we will allow for an additive individual vessel effect α_j, j=1,2, which permits differences in equipment and efficiency for the two vessels. This leads to the following model for the observations $\{y_{i,j}, i=1, \ldots, n; j=1,2\}$ where j=1, 2 corresponds to the first and second vessel in Table 1:

$$\begin{aligned} y_{i,1} &= f(x_{i1}, \ldots, x_{ip}) + \alpha_1 + \varepsilon_{i,1} \\ y_{i,2} &= f(x_{i1}, \ldots, x_{ip}) + \alpha_2 + \varepsilon_{i,2}. \end{aligned} \tag{1}$$

All the factors affecting jointly tow performance are supposed to be in the function f, and therefore the residuals $\{\varepsilon_{i,j}, i=1, \ldots, n; j=1,2\}$ are assumed to be independent zero-mean identically distributed random variables and $\sigma_\varepsilon = sd(\varepsilon_{i,j})$ is the measurement error.

We can now eliminate f and the explanatory variables by taking differences, i.e.

$$z_i = y_{i,1} - y_{i,2} = \alpha_1 - \alpha_2 + \varepsilon_{i,1} - \varepsilon_{i,2}.$$

The expected difference between the two vessels is then given by

$$E(z_i) = \alpha_1 - \alpha_2$$

and because of the independence of $\varepsilon_{i,1}$ and $\varepsilon_{i,2}$,

$$\sigma_z^2 = \mathrm{var}(z_i) = \mathrm{var}(\varepsilon_{i,1} - \varepsilon_{i,2}) = 2\sigma_\varepsilon^2,$$

and the standard error σ_ε can be estimated as

$$\hat{\sigma}_\varepsilon = \frac{1}{\sqrt{2}}\hat{\sigma}_z = \frac{1}{\sqrt{2}}\left\{\frac{1}{n-1}\sum_{i=1}^{n}(z_i - \bar{z})^2\right\}^{\frac{1}{2}}, \tag{2}$$

whereas $\delta = \alpha_1 - \alpha_2$ is estimated by $\hat{\delta} = \bar{z}$.

It should be noted that in the actual computation of $\hat{\sigma}_\varepsilon$ and δ, the data $y_{i;j}$ are log transformed, i.e.

$$y_{i,j} = \log(n_{i,j}/d_{i,j}),\ i = 1, \ldots, n; \qquad j = 1,2, \qquad (3)$$

where $n_{i;j}$ and $d_{i;j}$ denote the catch in numbers and the towed distance, respectively, for vessel j at the ith haul. Log-transformed data are used to reduce the heterogeneity of the variance.

Tests for differences between experimental groups

If our hypothesis, that parallel trawling experiments can be used to quantify a measurement error inherent in the cod catching process itself, is correct, we expect that this error, as estimated by $\hat{\sigma}_\varepsilon$, should be the same for all 10 experimental groups. If the z_i's originate from a Gaussian distribution, the null hypothesis of equal variance can be tested by Bartlett's test (*cf.* all groups tested simultaneously, Bickel and Doksum, 1977, p. 304) and if needed, followed by a series of F-tests where the groups are tested against each other in pairs.

The possible differences in efficiency caused by different vessels or fishing gears (or both) can be tested by an ANOVA test followed by a series of t-tests if the ANOVA test leads to rejection. Again, normally distributed observations are a prerequisite for such tests.

Our first task was therefore to check whether the z_i-data followed a Gaussian distribution. It seemed plausible to assume that observations from different groups followed the same distribution, but possibly with differences in mean and variance. Therefore, when checking for normality, we considered the standardized variables

$$x_i = \frac{z_i - \bar{z}_k}{s_k},$$

where, $k=k(i)$, $k=1, \ldots, 10$, denotes the group that haul i, $i=1, \ldots, n$, belongs to; and $\bar{z}_k$ and s_k are the average and the estimated standard deviation of the z-values in group k, respectively. Deviations from normality of $\{x_i\}$ can be checked visually by inspecting a normal plot, and formally by e.g. the Kolmogorov-Smirnov test (Bickel and Doksum, 1977, ch. 9.6).

Results

The log-catches $\{y_{i,j}\}$ and the corresponding differences $\{z_i\}$ are presented in Figure 1. The catches range from approximately $e^3 \approx 20$ to $e^8 \approx 3000$, but on the log-scale the difference in catch between the vessels does not seem to depend on the size of the catches (see formal test at the end of this section). A normal plot of the standardized observations $\{x_i=(z_i-\bar{z}_k)/s_k\}$ appears linear (Fig. 2) and the Kolmogorov-Smirnov test does not reject the null hypothesis of normality at a 10% level. Testing each group separately (except group 7 where the sample size is too small) yields the same result, i.e. normality is not rejected at a 10% level for any group, thus justifying the use of Bartlett, F- and t-tests. Bartlett's test for testing equality of variances yields a P-value of 0.81. In view of this, it is not really necessary to test the groups in pairs for equality in variance using an F-test, but as a source of additional information we have carried out the tests obtaining the lowest P-value of 0.078 for groups 4 and 5. Thus, based on these data, the hypothesis of a uniform measurement error independent of geographical location, time, depth etc., could not be rejected.

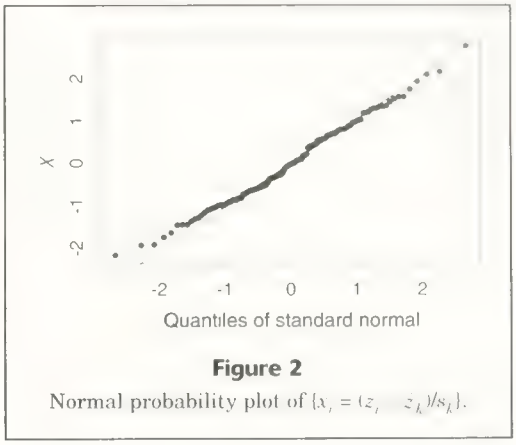

Figure 2

Normal probability plot of $\{x_i = (z_i - \bar{z}_k)/s_k\}$.

To investigate possible differences in efficiency for the participating vessels we did an ANOVA test. We found a P-value less than 10^{-7}, indicating significant differences. This finding was consistent with earlier findings in calibration experiments (Pelletier, 1998). Thus, because $E(Z_i)$ cannot be considered equal for all groups (also the confidence intervals in Fig. 1B), a pooled variance could be used for estimating σ_ε^2. Alternatively, z_i in Equation 2 could be replaced by the variables $z_i'=z_i-\bar{z}_k$, which are adjusted for group means and are identical to the residuals from the ANOVA fit. The resulting estimates with the last approach are $\hat{\sigma}_\varepsilon^2=0.069$ and $\hat{\sigma}_\varepsilon=0.263$. The bootstrapped standard errors of $\hat{\sigma}_\varepsilon^2$ and $\hat{\sigma}_\varepsilon$ are 0.0077 and 0.0147, respectively (1000 bootstrap replicates were used). Some caution should be exercised in interpreting these numbers (see e.g. Srivastava and Chan, 1989).

Compared with the total variability of the survey, the measurement error of a single haul is relatively small. For the last 5 years (1996–2000), var(y_i) for the nonzero catches varied between 1.38 and 2.06 for the winter survey and between 2.53 and 3.92 for the autumn survey. Thus, σ_ε^2 is about 2–5% of the total variation. This is the percentage of the variation that we cannot expect to be able to explain by explanatory variables. One should carefully note that these numbers are on the log scale. If antilogs of the catch rate were to be used, the additive model (Eq. 1) would have to be replaced by a multiplicative model, and the relative magnitude of variances would be changed.

The results for length-stratified data are shown in Table 2, as well as the results obtained by measuring the catches by weight instead of by numbers, i.e. by replacing $n_{i;j}$ in (Eq. 3) by, $m_{i;j}$, where $m_{i;j}$ is the weight of the catch in kilograms. Only hauls where both vessels

Table 2

Estimates of σ_ε^2 (with bootstrapped means and standard errors) for catches measured in kg (first column), total number of fish caught (second column), and catch of fish in various length-stratified groups measured in numbers (last four columns). The number of hauls where both vessels caught at least 10 cod is given in the fourth row, the groups excluded due to less than four remaining hauls are given in the fifth row, the average catch of the remaining hauls in the sixth row and *P*-values from Bartlett's test for equal variances, in the seventh row. The means and standard errors were estimated by using 1000 bootstrap replicates.

	kg	Total no of fish caught	Catch of fish in length stratified groups			
	>0 cm	>0 cm	<30 cm	30–59 cm	≥60 cm	≥30 cm
σ_ε^2	0.0744	0.0690	0.1124	0.0801	0.0855	0.0643
boot. mean of σ_ε^2	0.0740	0.0684	0.1113	0.0788	0.0844	0.0637
boot. SE of σ_ε^2	0.0096	0.0077	0.0140	0.0114	0.0122	0.0083
No. of hauls with at least 10 cod	130	130	113	117	103	118
groups excluded	none	none	2,3	10	2,7,10	10
v	1.77	5.28	4.61	4.06	3.61	4.52
P-value, Bartlett	0.11	0.81	0.31	0.87	0.60	0.97

collected 10 specimen or more were included, and only groups with at least four such hauls. The null hypothesis of equal variance was not rejected for any of the length groups (*P*-values from Bartlett's test are given in Table 2). It is seen that $\hat{\sigma}_\varepsilon^2$ is highest for small fish, and the bootstrapped standard errors indicate that the difference is statistically significant. Indeed, let $D = \hat{\sigma}^2_{\varepsilon,small} - \hat{\sigma}^2_{\varepsilon,large}$ denote the difference in measurement error between small (<30 cm) and large (≥30 cm) fish. If $\sigma^2_{\varepsilon,small}$ and $\sigma^2_{\varepsilon,large}$ are independent and normally distributed (their bootstrap distributions are approximately normal) with standard errors as given in Table 2, it follows that $D \sim N(0, 0.0140^2 + 0.0083^2)$ under the null hypothesis of equal measurement errors. The corresponding one-sided *P*-value for the observed D is 0.0016.

The hauls differed in towed distance, with the two most frequently recorded values being 1 and 1.5 nmi which correspond to 20 and 30 minutes tow duration. Stratifying on tow duration (which is recorded more precisely than towed distance), with hauls of less than 25 minutes duration (33%) in group A and the remaining hauls (67%) in group B, and estimating the measurement error for each group separately, we get $\hat{\sigma}_\varepsilon^2$=0.0707 and 0.0656 for group A and B, respectively. Thus, there is no significant difference due to tow duration. For fish less than 30 cm, the corresponding estimates are 0.115 and 0.107 for group A and B, respectively.

No significant relationship was found between the magnitude of the catches and their differences. A regression analysis was performed with the absolute value of the mean-adjusted differences in catch rate, $|z_t'|$, as the dependent variable and the average catch $\bar{y}_t = (y_{t,1} + y_{t,2})/2$ as the independent variable. The regression equation was $|z_t'| = 0.20 + 0.019 y_t$ and the *P*-value under the null hypothesis of no relationship was 0.31. However, the residuals from the analysis were skewed with a long right-hand tail; therefore a bootstrap test was also done, resulting in an empirical *P*-value of 0.137, and again the null hypothesis of no relationship was not rejected at a 5% level.

Discussion

We have estimated the measurement error (σ_ε^2) of a trawl haul by using data from parallel trawling experiments, including 130 parallel hauls from 10 groups of experiments. No significant differences in σ_ε^2 among the groups were found. Thus, σ_ε^2 seems to be independent of year, time of the year, and geographical position at which the haul was taken. It also seems to be independent of the catch size on a logarithmic scale. The magnitude of σ_ε^2 is small (≈2–5%) compared with the total variability in the survey trawl catches. The results are preliminary in that they are based on a limited set of hauls and more extensive experiments would be of interest to check their consistency. In another investigation, Pelletier (1998) examined the vessel effect between two research vessels. These data could possibly be used to test the general pattern revealed by analyses of data in the current study. Strømme and Iilende (2001) examined a total of 365 paired hauls from intercalibration experiments off Namibia in 1998 and 1999 between the research vessel *Dr. Fridtjof Nansen* and commercial trawlers. These data of Namibian hake (catch in kg/h) were kindly made available to us, and an estimate of $\hat{\sigma}_\varepsilon^2$=0.19 was obtained for the measurement error. The variance of y_t for all the 365 hauls was 2.0; the measurement error for this study on the log scale was about 10% of the survey variance.

Actually σ_ε^2 may be an overestimation of the measurement error because all the explanatory variables are not exactly the same for the two sets of measurements in Equation 1. For example the geographical location is not the same and the fish densities may differ from one vessel to the other because of the distance between them. However, because the towed distance is typically 5–10

times the distance between the vessels, we believe this factor to be of minor importance.

Another problem is the determination of the towed distance. The uncertainty connected with subjective judgments and inaccuracies in the GPS should be included in the measurement error because these factors are also present at a standard survey haul. However, it is not obvious to what extent the differences in the recorded towed distances are due to differences in subjective judgments or to differences in actual towed distances. In our calculations, we used the recorded values from both vessels for $d_{i,j}$. If there is no real difference in the towed distances within a comparison, $\hat{\sigma}_\varepsilon^2$ is expected to decrease by setting $d_{i,1}=d_{i,2}$ for all hauls, thus eliminating one factor of uncertainty. At the other extreme, if the subjective judgments are perfect, and the recorded differences in towed distance are due to real differences, one would expect $\hat{\sigma}_\varepsilon^2$ to increase by setting $d_{i,1}=d_{i,2}$, because an extra error then is added. Actually, by using the values from vessel 2 only and by setting $d_{i,1}=d_{i,2}$ the resulting estimate of σ_ε^2 is $\hat{\sigma}_\varepsilon^2=0.061$, which is a reduction by about 11%. Even though this value is statistically insignificant, it indicates that uncertainty connected to the measurement of towed distance constitutes a part of the measurement error (see also Godø et al., 1990).

In the "Results" section, the null hypothesis of equal efficiency for all the participating vessels was rejected. By joining data from the groups where the same pair of vessels participates, the ability to detect differences in efficiency between the vessels increases through an increased sample size and a smaller number of simultaneous tests (with N tests and a nominal level α, the null hypothesis of equal efficiency is rejected for P-values smaller than the Bonferroni corrected level α/N). For the N=6 tests, we obtained P-values 0.0005 for group 4, 0.009 for groups 1 and 2, 0.011 for groups 6 and 10, 0.034 for groups 5 and 9, 0.107 for groups 7 and 8, and 0.123 for group 3. With a level α=0.05 we have $\alpha/6$=0.0083, and for group 4 the difference is clearly statistically significant. The higher efficiency of *Jan Mayen* (JM) in this group was probably due to her heavier trawl doors. At a 10% level, the vessel *Anny Kræmer* (LIZY) was significantly more efficient than *Johan Hjort* (JH) in groups 1 and 2, and *Michael Sars* (MS) was significantly more efficient than JH in groups 6 and 10. The differences between *G.O. Sars* (GS) and JH (groups 5 and 9), GS and JM (groups 7 and 8) and GS and LIZY (group 3) were not significant. However, excluding group 4, and ignoring statistical significance, the vessels can, in fact, be ranged consistently after increasing efficiency as

$$JM \xrightarrow{7,8} GS \xrightarrow{5,9,3} JH \xrightarrow{1,2,6,10} LIZY \,/\, MS. \quad (4)$$

The numbers in parentheses refer to experiment groups, and for each group one vessel to the left, and one to the right of the corresponding arrow, are involved, the one to the right being always the most efficient one.

There also seems to be a significant difference in the measurement error for small and large fish, it being higher for small fish. One explanation may be that the interaction between small fish and the trawl gear is more variable (Godø and Walsh, 1992); another possibility is that small fish operate more in patches than do large fish. If the last assumption is correct, a reduction in σ_ε could be expected with increasing tow length. However, for the set of tows considered, we found no significant difference in σ_ε due to tow distance.

Consistent with the length dependency of the measurement error is the length dependency of the total variability of the surveys. The average var(y_i) for the winter surveys 1996–2000 for fish ≤31cm and ≥64cm, was 2.49 and 0.98, respectively; whereas for the unstratified data it was 1.66. The corresponding numbers for the autumn surveys 1996–2000 were 3.03, 1.47, and 2.98 for small, large, and unstratified fish, respectively. All numbers are for nonzero catches.

Trawl catches have been considered highly variable (see e.g. Gulland, 1964; Doubleday and Rivard, 1981) and as a result the reliability of trawl survey estimates have been questioned. Abrupt changes in catch size and composition over a short time in a limited area have demonstrated the difficulties in using the information as a relative estimate of density without an understanding of the nature and causes of the variability (Godø, 1994). Unexpected annual changes in survey indices may also be a problem for a reliable evaluation of fish stocks and can be attributed to a variable bias (changes in catchability) among years (Pennington and Godø, 1995). Our analysis demonstrates that for the bottom trawl survey in the Barents Sea, catch rates and composition from the applied survey trawl are repeatable up to a relatively small and constant measurement error and are hence expected to give a reliable picture of the relative fish density at a given site and time. Further, the measurement error of this sampling gear is small compared with the total observed variability. For a particular survey it appears that most of the survey variance is caused by station-to-station differences in catches rather than local conditions at a station. This may be taken as an indication that shorter and more frequent tows may be more efficient for monitoring this cod stock. Moreover, when controlling trawl geometry (Godø and Engås, 1989) and towed distance (Godø et al., 1990), it should be possible to establish explanatory factors to be included in the survey assessment procedure. To the degree that one is able to establish models to determine fish densities at any station, the comparability of density measures throughout the distribution area will improve. The consequences will thus not only be more reliable survey estimates, but we also expect a better understanding of distributional patterns in relation to the physical and biological environment.

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Abstract—Reproductive organs from 393 male and 382 female porbeagles (*Lamna nasus*), caught in the western North Atlantic Ocean, were examined to determine size at maturity and reproductive cycle. Males ranged in size from 86 to 246 cm fork length (FL) and females ranged from 94 to 288 cm FL. Maturity in males was best described by an inflection in the relationship of clasper length to fork length when combined with clasper calcification. Males matured between 162 and 185 cm FL and 50% were mature at 174 cm FL. In females, all reproductive organ measurements related to body length showed a strong inflection around the size of maturity. Females matured between 210 and 230 cm FL and 50% were mature at 218 cm FL. After a protracted fall mating period (September–November), females give birth to an average of 4.0 young in spring (April–June). As in other lamnids, young are nourished through oophagy. Evidence from this study indicated a one-year reproductive cycle and gestation period lasting 8–9 months.

The reproductive biology of the porbeagle shark (*Lamna nasus*) in the western North Atlantic Ocean

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The porbeagle (*Lamna nasus*), a pelagic shark in the family Lamnidae, inhabits the cold temperate waters of the North and South Atlantic, South Pacific, and southern Indian Oceans, as well as the subantarctic region of the Southern Ocean (Svetlov, 1978; Compagno, 1984). In the western North (NW) Atlantic Ocean, the porbeagle ranges from the Flemish Cap and the Grand Banks off southern Newfoundland, Canada, to the Gulf of Maine and (rarely) south to New Jersey (Templeman, 1963; Compagno, 1984). The porbeagle is most commonly encountered from the Gulf of Maine to the Grand Banks, where it has been the subject of a commercial fishery since 1961 (O'Boyle et al.[1]; Campana et al[2,3]). Seasonal abundance is related to north–south migrations (Aasen, 1963; Campana et al.[3]; Aasen[4]).

Lamnid sharks are ovoviviparous and nourish their embryos by oophagy (Lohberger, 1910). Early descriptions of porbeagle embryos exhibiting oophagy were documented by Swenander (1907) and Shann (1911, 1923), and more recently by Francis and Stevens (2000). Litter size has been variously reported as one to five pups (Dunlop, 1897; Swenander, 1907; Shann, 1911, 1923; Gauld, 1989; Francis and Stevens, 2000). Birth size has been reported as

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[4] Aasen, O. 1961. Some observations on the biology of the porbeagle shark (*Lamna nasus* L.). ICES C.M. Copenhagen 1961, Near Northern Seas Committee 109:1–7.

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60–80 cm total length (TL) (54–72 cm fork length [FL]) (Shann, 1923; Compagno 1984, Francis and Stevens, 2000). Bigelow and Schroeder (1948) speculated that females are gravid by 152 cm TL (136 cm FL), whereas Aasen (1963) concluded that females mature between 200 and 250 cm TL (193–240 FL) and males mature between 150 and 200 cm TL (146–193 FL). In a more comprehensive study, Francis and Stevens (2000) found that females mature between 165 and 180 cm FL in the South Pacific.

In this study, we present the results of a comprehensive examination of porbeagle reproduction in the NW Atlantic Ocean. We define the sizes and stages of maturity for both sexes and provide insights into the reproductive cycle, as well as embryo sex ratios and litter sizes. These parameters will be useful for the refinement of fishery management plans for the porbeagle shark in the NW Atlantic Ocean.

Materials and methods

Porbeagles were collected with pelagic longline onboard both U.S. and Canadian commercial fishing vessels and U.S. research vessels fishing in U.S. and Canadian waters from the Gulf of Maine and Georges Bank (northeastern U.S.) to the Grand Banks off southern Newfoundland. Several specimens were obtained at a sport-fishing tournament held on Stellwagen Bank, Massachusetts. Sampling took place between 1979 and 1999, but most of the data were obtained during 1993, 1994, and 1999.

Morphometrics

For each shark, five lengths were measured over the curve of the body to the nearest half centimeter (cm): interdorsal length (posterior dorsal fin base to origin of second dorsal fin; IDL); dorsal length (origin of first dorsal fin to precaudal pit; DL); precaudal length (snout to precaudal pit; PCL); fork length (snout to fork of tail; FL); and total length (snout to a perpendicular line from the tip of the upper caudal fin in a natural position; TL). Total length of embryos were measured along a straight line with the tip of the tail fully extended (TL_s) because of the difficulty in obtaining over-the-body or FL measurements (or both) in embryos less than 6 cm TL. FL and PCL were taken when possible. FL are reported for all sharks in our study; TL values are presented for embryos with calculated or measured FL in parentheses. TL can be converted to FL by using the following regression (Campana et al.[3]):

$$FL = 0.885(TL) + 0.99 \qquad [r^2=0.99, n=361].$$

All other length and weight conversions can be found in Campana et al.[2] Aasen's (1963) TL values were converted to FL by using the approximate formula:

$$FL = 0.947^{*}(AasenTL) + 3.64 \text{ (Campana}^{5}\text{)}.$$

TL_s can be converted to FL for embryos by using the regression

$$FL = 0.832(TL_s) - 0.19 \qquad [r^2=0.99, n=131].$$

Whole weight in kilograms (kg) was taken when possible. Literature values of TL were converted to FL for comparison and the conversions are presented throughout the text in parentheses. The converted values from the literature should be considered good estimates only because of the variation in measurement techniques between studies.

Maturity indicators

A number of measurements, weights, and conditions were taken on reproductive organs in both sexes to develop indices of maturity following Pratt (1979, 1993, 1996). Most specimens were measured fresh; however, some frozen reproductive tracts were also measured. Reproductive tracts were measured on the right side of the specimen. Organ terminology follows Pratt (1979) (Fig. 1, A and B).

For more detail, uteri were divided visually into anterior and posterior segments. The anterior segment is defined as the portion between the origin of the uterus at the isthmus and the point where both uteri join. The posterior segment is the portion from the junction to the posterior constriction of the uterus (Fig. 1B). A length measurement was taken for the anterior uterus, and width was taken midway along this portion of the uterus.

Active ovulation was defined as occurring if 1) ova were entering the ostium or were present inside the upper oviduct, 2) ova and capsules were present in the oviducal gland, 3) encapsulated ova were present in the isthmus, and 4) encapsulated ova were present in the uterus.

Prior mating activity was assessed according to the presence or absence of a vaginal membrane (hymen), determined by passing a probe through the posterior end of the uterus into the cloaca. The presence of vaginal mating scars was used to determine if recent mating had taken place. Scars were identified as either healed or recent. Maturity status of both sexes was assigned to each shark based on all reproductive organ characteristics (Pratt, 1979). The size at 50% maturity was determined by fitting a logistic regression to a plot of percent maturity versus FL.

Embryos were either frozen or preserved in 10% buffered formalin. Litter size and embryo sex were determined in the field or in the laboratory under a dissecting microscope. Embryo growth was related to month. Linear regressions were fitted to the relationship between mean embryo length and month for samples from the NW Atlantic and southwest Pacific Oceans and compared with analysis of covariance (ANCOVA).

Results

Male length at maturity

Reproductive data were obtained from 393 male porbeagle sharks ranging in size from 86 to 246 cm FL, of which

[5] Campana, S.E. 2000. Unpubl. data. Department of Fisheries and Oceans, Bedford Institute of Oceanography, P.O. Box 1006, Dartmouth, Nova Scotia, Canada, B2Y 4A2.

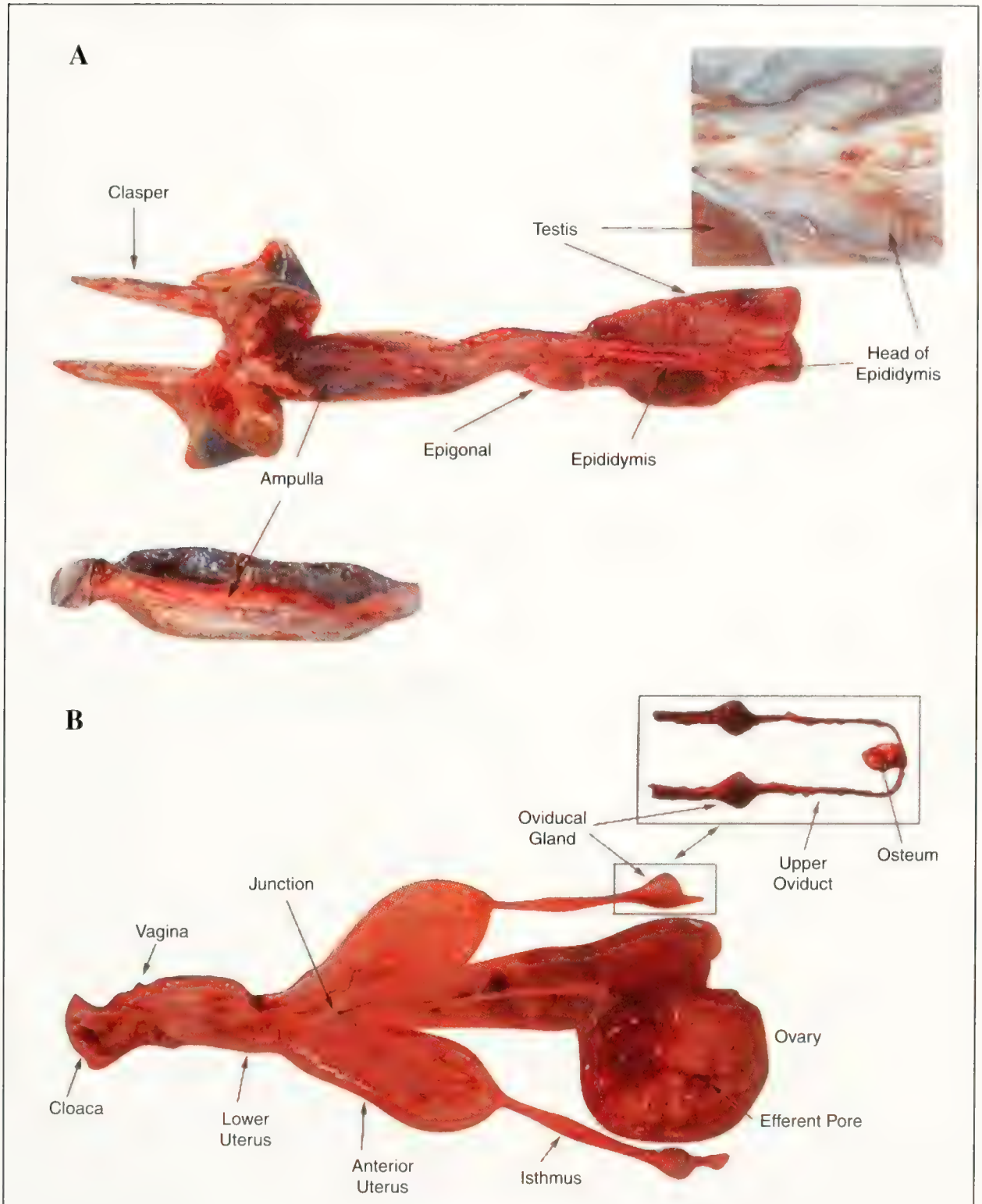

Figure 1

Reproductive systems of the porbeagle shark: (**A**) male reproductive tract with closeup inserts of the head of the epididymis and the ampulla epididymis and (**B**) female reproductive tract with a closeup of the upper oviduct leading into the ostium.

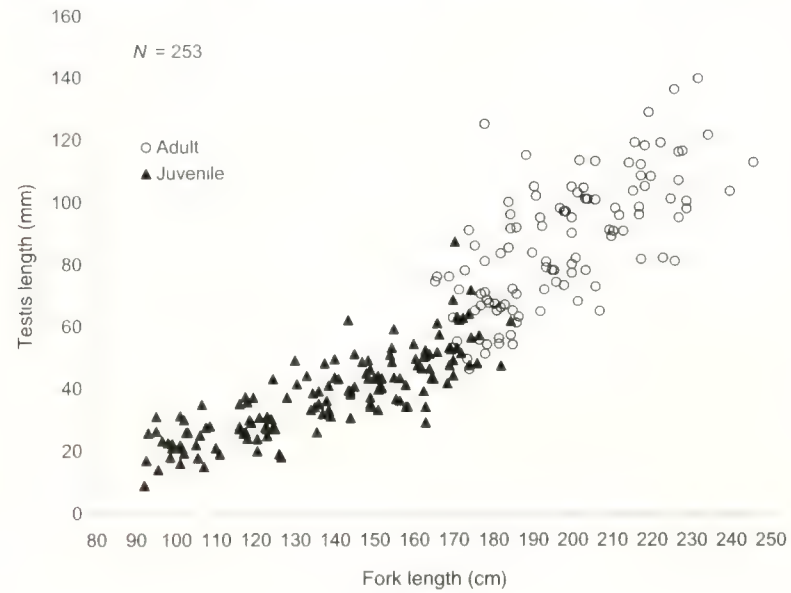

Figure 2

Relationship of right testis length to fork length.

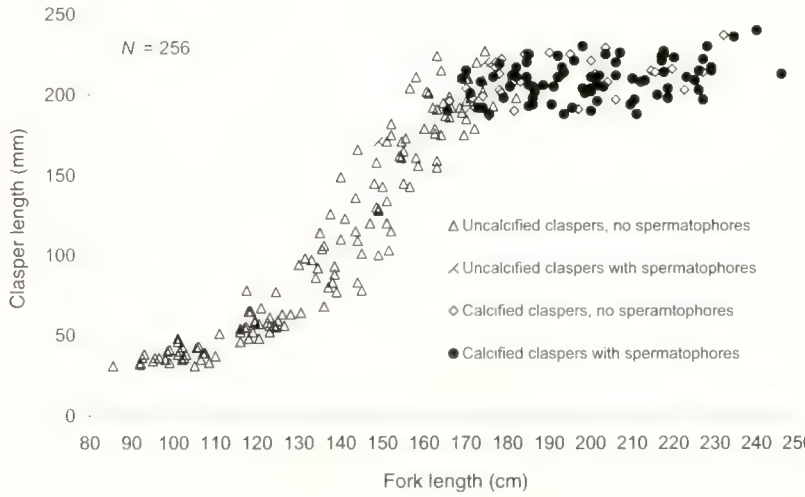

Figure 3

Relationship of right outer clasper length to fork length. Relative amount of clasper calcification and presence or absence of spermatophores are also indicated.

reproductive organs were measured for 267. Development of the siphon sacs, as well as internal male reproductive organs—testes (diameter and length), epididymis, and ampulla epididymis—is gradual in relation to FL (Fig. 2). The development of the claspers, however, shows a distinct inflection (Fig. 3). Claspers begin to elongate when the males approach 120 cm FL, and rapid clasper growth begins at 135 cm FL and slows by about 170 cm FL when they have reached their maximum adult size of 19–24 cm. The largest shark with uncalcified claspers but containing spermatophores in the ampulla epididymis was 176 cm FL, and the smallest shark with calcified claspers, but with no spermatophores, was 166 cm FL. Claspers rotate freely at all sizes in the porbeagle; therefore clasper rotation is not a good measure of maturity. Males of 135 to 184.5 cm FL are in a transitional phase leading to maturity. At this stage, claspers are lengthening and the head of the clasper (rhipidion) is beginning to develop, whereas at 149 cm FL

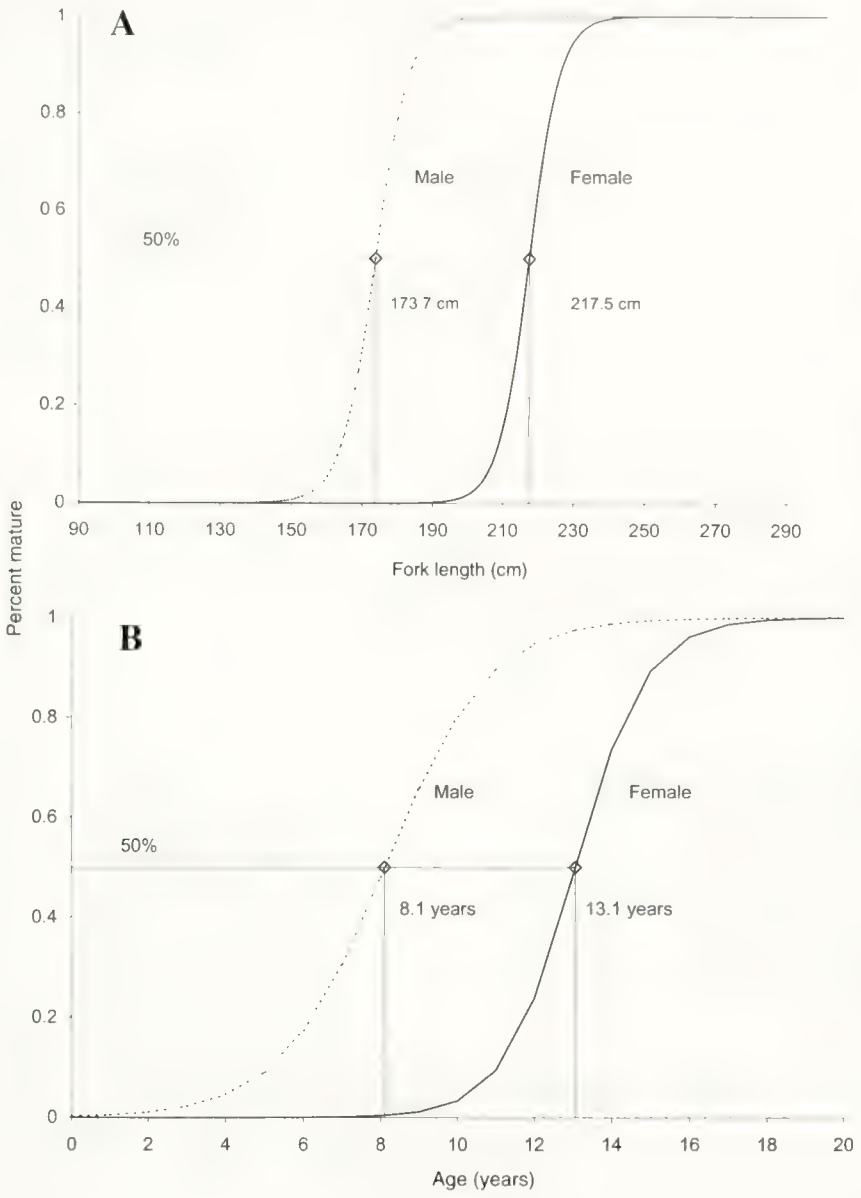

Figure 4

Maturity ogives for male and female porbeagle sharks: (**A**) ogives based on length, (**B**) ogives based on age. Fifty percent maturity is indicated.

and greater, spermatophores appear in the ampulla epididymis. By 162 cm FL fully calcified claspers were observed. Individual variation exists in body length and the order in which these developments take place. All males observed were mature by 185 cm FL based on clasper calcification and the ability of the rhipidion to open. The presence of spermatophores may be used in addition; however, absence of spermatophores can be attributed to season as well as to maturity. Each clasper bears a sharp, conical, calcified spur near the tip which folds out of the distal surface as the rhipidion opens. In adults, the sharp spur tip was either covered by an epidermal membranous sheath, or naked. A naked spur is an indicator of mating activity because mating ruptures the sheath. The FL at which 50% of the male population is mature, based primarily on clasper condition, was estimated as 174 cm FL (Fig. 4A).

Both testis size and the amount of spermatophores in the ampulla epididymis showed distinct fluctuations related to the mating season. From November through mid December, the testis lobes were noticeably reduced in diameter, the testes were smaller, and the epigonal organ had infiltrated the space previously occupied by the

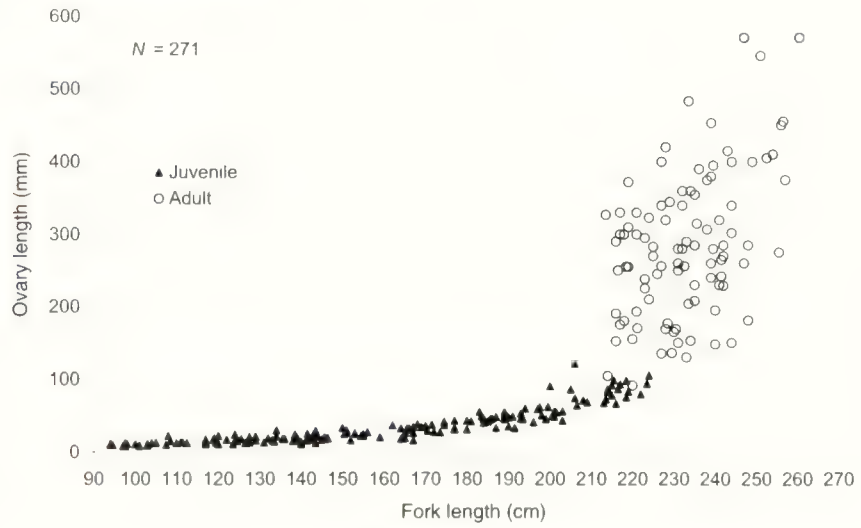

Figure 5

Relationship between ovary length (mm) and fork length (cm) in the porbeagle shark. Juveniles and adults are indicated.

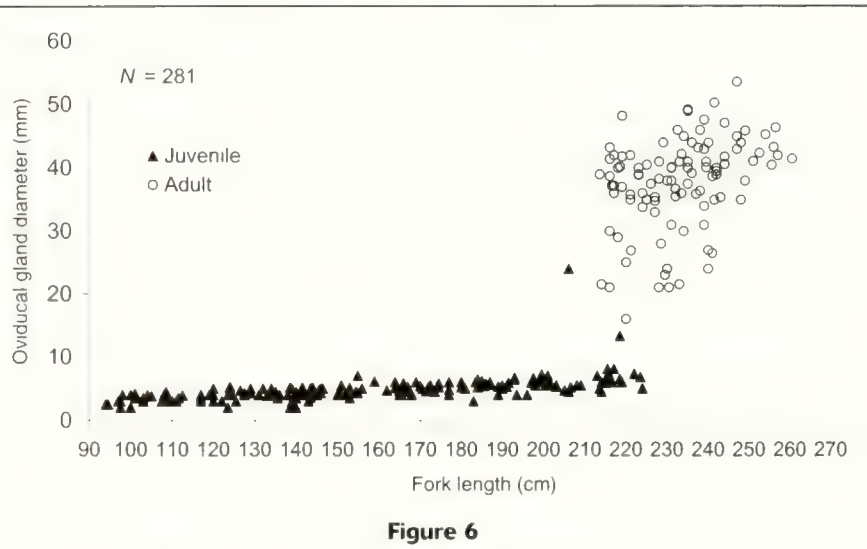

Figure 6

Relationship between oviducal gland diameter (mm) and fork length (cm) in the porbeagle shark. Juveniles and adults are indicated.

testes. Spermatophores in the ampulla epididymides were at their greatest volume in September–December; in February–May relatively few spermatophores were observed, and by June the concentration started to increase.

Female length at maturity

Reproductive data were obtained from 382 female porbeagle sharks ranging in size from 94 to 288 cm FL, of which reproductive organs were measured for 284. The relationship between the measurements of internal reproductive organs (ovary length and width, anterior uterus length and width, and shell gland (oviducal gland) width to FL) showed a sharp increase between 210 and 220 cm FL (Figs. 5 and 6). Oocytes are not visible to the naked eye in juveniles less than about 200 cm FL, and in larger, immature females, small, clear, yolkless oocytes range in size from 0.5 to 3.7 mm in diameter. In mature females, vitellogenic oocytes range from 2.2 to 7.0 mm. The increase in oocyte diameter, as well as the development from clear yolkless oocytes to vitellogenic oocytes, occurs between 210 and 225 cm FL (Fig. 7). Criteria for maturity in female porbeagles include the presence of embryos or fertilized ova in the uteri, and indications of past pregnancy, such

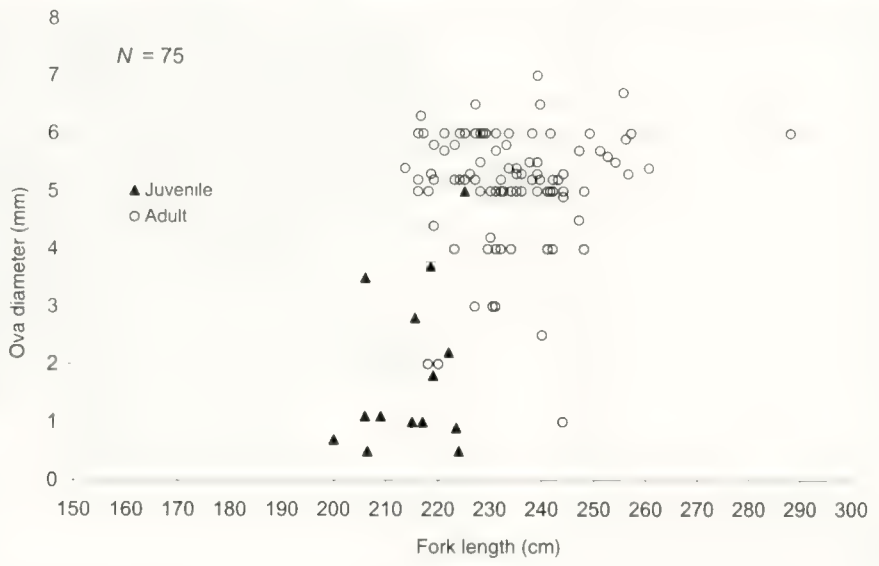

Figure 7

Relationship between maximum **ovum?** diameter (mm) and fork length (cm) for the porbeagle shark.

as flaccid uteri with trophonemata and reduced ovaries containing few maturing or mature oocytes. Juvenile females have small undeveloped ovaries with white to clear oocytes; the uterus appears narrow and constricted, and the oviducal gland is seen as a barely perceptible widening of the oviduct. The juvenile and mature virgin sharks that we examined had a membrane separating the vagina from the cloaca, whereas mature (reproductively active) sharks had no membrane. In nongravid females, maturity is based on the presence of mature oocytes in a developed ovary, an expanded uterus, a well-developed oviducal gland, internal and external mating scars, and the absence of a vaginal membrane. The smallest mature female in our sample was 210 cm FL based on the absence of a vaginal membrane and the condition of the internal reproductive organs, and the largest immature female was 230 cm FL based on the presence of a vaginal membrane and internal organ condition. Fifty percent of the female porbeagle population was mature at 218 cm FL (Fig. 4A).

Mating injuries

Fresh mating scars, containing at least small areas of unhealed dermal lacerations, were observed from late September through mid-December, during which time most adult females appeared to have recently mated or were in the early stages of pregnancy. Scars and cuts were often observed on either or both pectoral fins as single or multiple jaw outlines, and the trailing edge of the fin was often shredded. Tooth scrape marks, puncture wounds, and gouges, some as open, penetrating subdermal lacerations, were observed mainly along the posterior lateral, dorsal, or ventral body surface. None of the wounds appeared to have penetrated the abdominal wall nor were they debilitating. No infected or necrotic tissue was seen in these wounds. Most mature female porbeagles had distinct fresh or healed mating scars.

Internal mating scars were observed on the vaginal walls from late September through mid-December. The scars were generally small, round to ovoid, hematose marks on an otherwise white to light yellow vaginal wall. These were probably caused by the spur that holds the clasper in place during copulation.

Gravid females, embryo growth, and nutrition

Data from 80 litters and 309 embryos were obtained from gravid females sampled from mid-September through April. In addition to embryos, these females had several different types of egg capsules in their oviducal gland, isthmus, and uteri. These were empty capsules, capsules containing one large ovum without a visible embryo (single ovum capsules), capsules with one developing embryo and attached yolk sac, capsules with 22–45 blastodisc-stage ova, and capsules containing 8–100 nonblastodisc-stage ova (nutritive capsules), some appearing atretic and in which individual ova were difficult to detect. The number of capsules present in each uterus ranged from none to 63 (Fig. 8).

The proportion of mature nongravid females with recent mating scars, but no obvious fertilized ova, decreased from September through December, whereas the proportion of gravid females increased (Fig. 9). All mature females examined in December were gravid. During October, several mature females contained either parts of, or entire, spermatophores in the uteri, but no ova capsules, indicating

that mating had taken place but that ova were not yet fertilized. On the basis of the occurrence of early-stage gravid females, the ripe condition of the males, and the presence of recent mating scars, we concluded that most mating occurs from late September through November. Mature males with copious amounts of spermatophores and mature females were captured on the same gear numerous times during the fall.

The right uterus of the one gravid female observed during late September had one single ovum capsule with no visible embryos, along with several blastodisc or nutritive capsules, whereas the contents of other uterus appeared to have been aborted. This was the only recently mated female observed in September. Some gravid females in October and November contained capsules with a single ovum, 6–7 mm diameter, in addition to varying numbers of empty, blastodisc, or nutritive capsules. These single ovum blastodisc capsules (usually two per uteri) were considered to be the annual developing embryos, their single ovum larger than those of the aggregate blastodisc or nutritive capsules. Gravid females examined during October had either single ovum capsules or embryos 0.9–6.8 cm TL_s (0.6–5.3 cm FL), and those seen in November had a decrease in occurrence of single-ovum capsules, and embryos ranged from 1.1 to 37.8 cm TL_s (0.7–31.2 FL). No gravid females with single ovum capsules were seen during December, and embryos ranged from 2.3 to 43.1 cm FL (Fig. 10). Only one nearterm, gravid porbeagle, caught in mid-April, was examined in our study. This shark had three embryos ranging in size from 59 to 72 cm TL_s (50–59 cm FL). The considerable variation in embryo length among litters during early gestation indicates a protracted mating season.

Postpartum females were observed from the first week of May to the first week of June. Our data from these females suggested that parturition extends from early April through early June. The presence of postpartum females in May–June after the September–November mating indicates a gestation period of about 8–9 months.

Although numerous gravid females are present from late September through December on the Scotian shelf and Grand Banks region, mature gravid or nongravid female sharks are seldom seen from January through June in the Canadian fishery. Gravid females were caught between Georges Bank and the Grand Banks (Fig. 11).

Fecundity

Embryos were found to be at the same developmental stage in each female, although embryo size varied as much as 14.6 cm in one litter. Runts were encountered in five females and although clearly developing, were considerably smaller than the coexisting embryos. Fecundity was calculated by using all embryos. The average number of embryos per porbeagle was 4.0 (304 embryos from 76 litters) although litters ranged from 3 to 6. In 66 litters there were two embryos per uterus. The sex ratio of 202 embryos (99 male and 103 female) was not significantly different from one (χ^2=0.08, P>0.1).

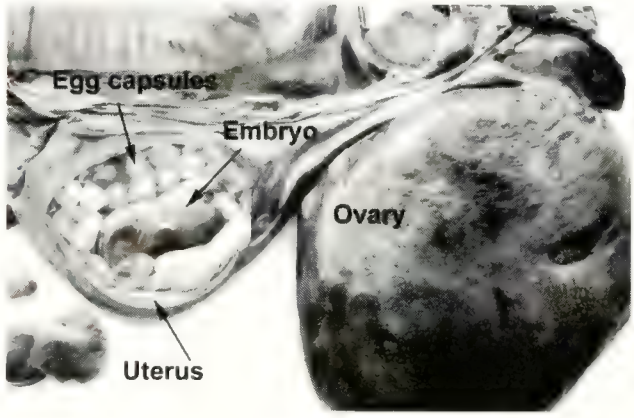

Figure 8

Photograph of an ovary and open uterus of a gravid porbeagle showing a developing embryo amid ova capsules.

In the uteri of six females, fertilized ova were found in the same ova capsule with one to three late developing yolksac embryos. Some of these fertilized ova appeared to be decomposing. These capsules were in the same uteri as a larger, developing litter, but the size of the embryos associated with the capsules (averaging 4–20% of the average size of the developing litter) were smaller than runts (runts averaged 24–43% of the average size of siblings) or the main litter. Because of their small size in relation to the developing litter, and their appearance of decomposition, it was presumed that they were ova that had been fertilized late by remaining sperm and that had probably not continued to develop. However, this is not to rule out the possibility that some of these embryos could have developed into runts or be consumed when littermates initiated feeding on egg capsules. Further research is being conducted on this subject and will be reported at a later date.

Embryonic development and growth

Newly fertilized ova, without visible embryos, were 6–7 mm in diameter. As the embryo developed, their yolk sacs decreased in size, and by the time the embryos were between 4.2 and 9.2 cm TLs (3.3–4.5 cm FL), the yolk sacs were tiny, white, ovoid structures attached to the embryo by a short stalk. Embryos were found in capsules up to 4–4.2 cm TL_s (3.1–3.3 cm FL). The smallest posthatch embryos were 3.2–4.2 cm TL_s (2.5–3.3 cm FL). The abdomens of posthatch embryos between 4.7 and 5.1 cm TL_s (3.7 and 4.0 cm FL) were slightly swollen. Functional embryonic dentition appeared in embryos at 12 cm TL_s (9.8 cm FL). As the embryo continues to grow, the yolk stomach increases in size as a result of *in utero* consumption of ova capsules by the embryo. The stomach becomes grossly distended by the time the embryo reaches 27–43 cm TL_s (23–36 cm FL). The large amounts of yolk material in the stomachs of these embryos was characteristic of oophagy. Frequently, parts of ova capsules, parts of, or whole, ova, and white flocculent material were observed in the clear intrauterine fluid surround-

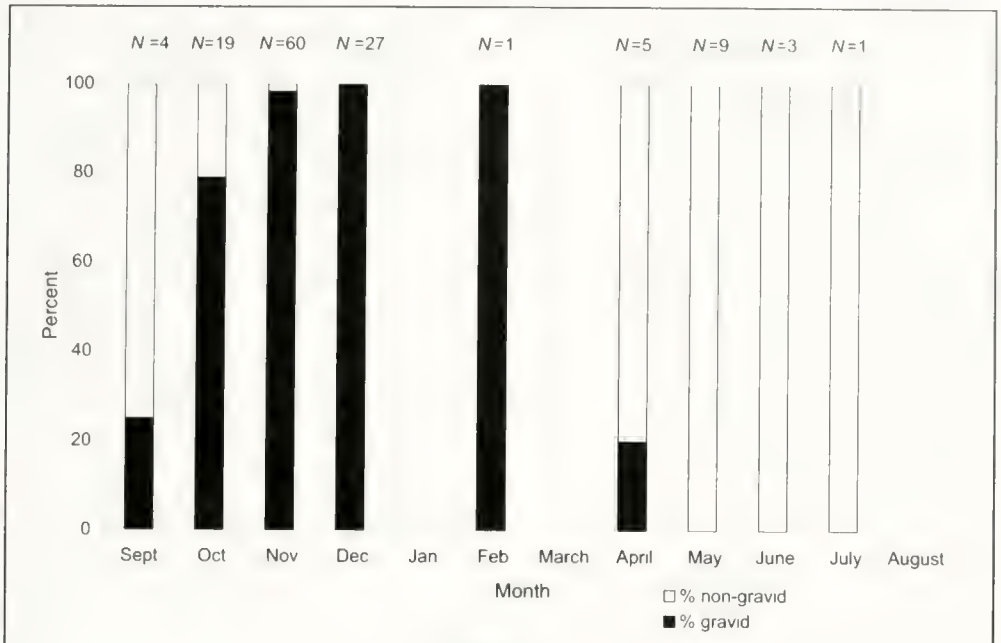

Figure 9

Relationship of gravid to nongravid adult female porbeagle sharks by month from 1979 to 1999.

ing the embryos, suggesting recent embryo feeding. One embryo was seen with a whole, undamaged ova capsule protruding from its mouth. The stomach contents of embryos from several litters did not show parts of other embryos, suggesting that adelphophagy (competitive embryonic cannibalism), found in the sandtiger shark (Gilmore et al., 1983) does not occur in the porbeagle. The existence of developing runts in several litters and consistently two embryos per uterus reinforces these observations. A slight modification to our knowledge of oophagy would be the possible consumption of the late-fertilized ova capsules that had small undeveloped and decomposing embryos along with unfertilized ova, as mentioned previously. Most gravid porbeagles examined during this study were ovulating and, therefore, nourishing their embryos. The times at which ovulation ceases, ovary size decreases, and the large amount of yolk in the stomach is consumed, need further definition.

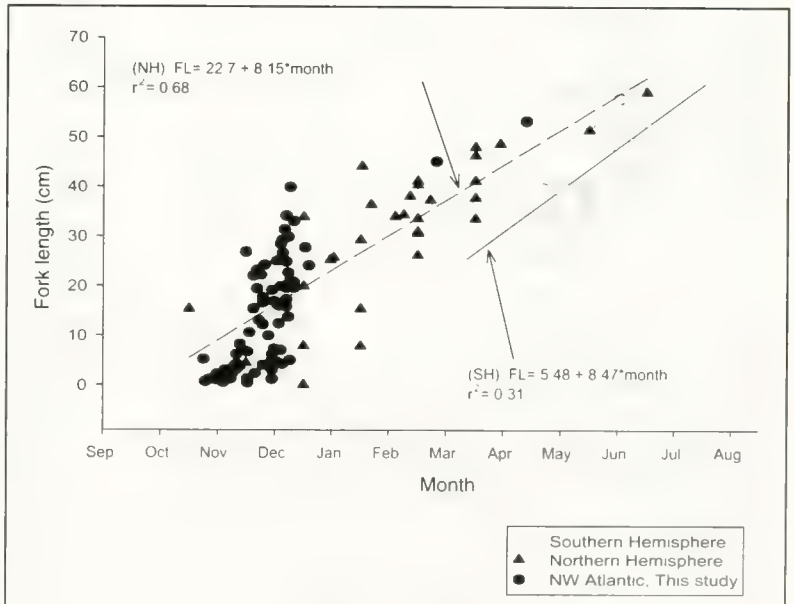

Figure 10

Monthly variation in mean lengths of embryo litters from both hemispheres. Data indicated by open circles and closed triangles are from Francis and Stevens (2000) and Francis,[6] respectively.

The mean growth rate of embryos from this study was 11.4 cm per month; however, this is most likely inflated by the lack of larger embryos. Combining data from the present study with previous data from the North Atlantic, which includes later term embryos (Francis and Stevens, 2000), leads to an estimate of 8.15 cm per month. The regression of growth per month for the North Atlantic embryos was significantly different from that of the South Pacific population in intercept (time of year) but not in slope (growth rate) (ANOVA $P>0.10$ slopes, $P<0.1$ intercept) (Fig. 10).

Neonates and young of the year

The smallest free-swimming porbeagle examined during this study was 77.5 cm FL (87 cm TL) on 24 May. Other records of free-swimming individuals measured in April–June, ranged from 55 to 79 cm FL (mean=71 cm FL, n=9)

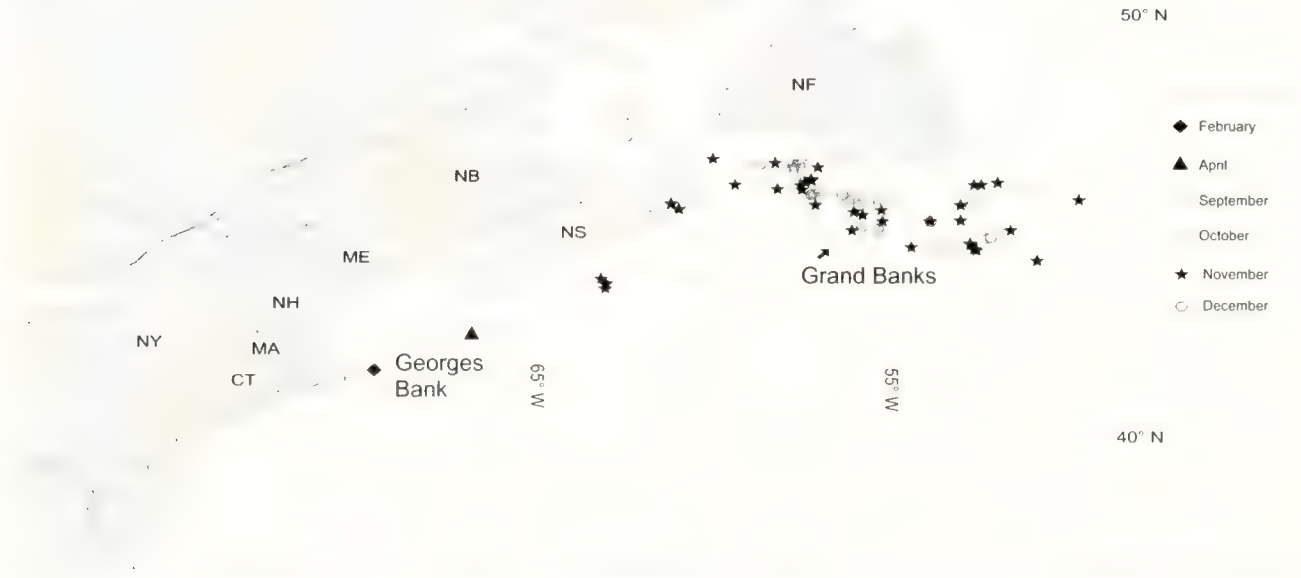

Figure 11

Map of the capture locations of all gravid female porbeagles by month of capture. Approximate locations of Georges Bank and the Grand Banks are indicated.

(Kohler[6]). The largest embryos in our study from one litter in April were 49–60 cm FL (59–72 cm TL).

Discussion

In the NW Atlantic, male porbeagles mature between 166 and 184 cm FL, and 50% maturity was at 174 cm FL, which corresponds to an age of 8 years (Fig. 4B; Natanson et al., 2002). The most accurate means of determining male maturity is clasper length and calcification. Because of the distinct seasonal variability, the presence of seminal products alone, is not a good indicator of maturity. Clasper rotation occurred at all sizes, eliminating it as a maturity indicator. Our estimate of length at maturity substantially refines Aasen's[4] estimate of 150 to 200 cm TL (146–193 cm FL) for this population. Aasen[4] based his estimates on clasper length in relation to dorsal length.

Female NW Atlantic porbeagle sharks mature between 210 and 230 cm FL and 50% maturity was at 218 cm FL, at an age of 13 years (Fig. 4B; Natanson et al., 2002). The sizes of all female reproductive organs measured showed a definitive inflection at maturity in relation to body size and are good indicators of maturity. Aasen[4] estimated female maturity between 2.0 and 2.5 m TL (193–240 cm FL) based on uterus length. Our estimates compare well to the upper part of his range; however our data do not support his lower size at maturity.

The seasonality of spermatophore production, observations of females with fresh mating scars, and observations of males and females on the same longline indicated that porbeagles mate in the fall, primarily between September and November. In an earlier study, sperm in the shell gland of a female, and the presence of a male caught on the same longline set in October, also suggested a fall mating period (Pratt, 1993). Aasen (1963) proposed a fall mating season (September–October) based on an increase in the amount of sperm present in the males "towards the end of August." This period agrees with the suggestion of a long mating season in the SW Pacific porbeagle population (Francis and Stevens, 2000). During this time, females have fresh external mating scars, internal vaginal scars, and spermatophores in the uterus. Gauld (1989) suggested that mating occurs during December–January in the northeast Atlantic on the basis of fresh mating scars on the pectoral fins.

Mating injuries have been documented for many species of sharks. Bite marks on females during mating have been documented in the blue (*Prionace glauca*), nurse (*Ginglymostoma cirratum*), sandtiger, (*Carcharias taurus*), blacknose (*Carcharhinus acronotus*) finetooth (*C. isodon*), blacktip (*C. limbatus*), sandbar (*C. plumbeus*), and Atlantic sharpnose (*Rhizoprionodon terraenovae*) sharks (Stevens, 1974; Gilmore et al., 1983; Schwartz, 1984; Castro, 1993, 1996, 2000). Fresh bite marks may coincide with insemination and ovulation, marking the approximate beginning of the gestation period (Parsons, 1983; Castro, 1996). Matthews (1950) noted lacerations in the vagina of the basking shark (*Cetorhinus maximus*) from the clasper spur. Pratt (1979) also observed abrasions from claspers in the vagina of female blue sharks.

Gravid females typically carry single-ovum capsules from September to November, and developing embryos from October to April. Aasen (1963) reported no gravid porbeagles from July to September 1961, in the NW At-

[6] Kohler, N. K. 2000. Unpubl. data. NMFS Apex Predators Program, 28 Tarzwell Dr., Narragansett, RI 02882.

lantic. Bigelow and Schroeder (1948) described gravid porbeagles in the Gulf of Maine during November, January, and August, although the latter month conflicts with both the present findings and those of Aasen (1963). Aasen (1963) reported that pregnant females carrying large embryos were observed in late May at the Flemish Cap. Templeman (1963) reported three gravid females from the SW Grand Banks during January and February 1953–56. Gauld (1989) reported the presence of gravid females from December to June in the NE Atlantic ocean, whereas Francis and Stevens (2000) reported gravid females from March to July in the SW Pacific Ocean.

Length variability within and between litters has been found in most porbeagle studies (Fig. 10). We found a difference of up to 14.6 cm in the lengths of individuals in one litter. Gauld (1989) found length differences of up to 11 cm within individual litters, and Shann (1923) found a 12–15 cm difference in embryo length within individual litters. Runts were observed in pregnant porbeagles in our study as well as by Francis and Stevens (2000).

As with other lamnids, female porbeagle sharks nurture their young through oophagy. Upon hatching from the single-ovum capsules and after absorption of the external yolk sac, embryos begin orally feeding on yolk-filled nutritive ova capsules. As a result, the internal yolk stomach of the embryos expands to the large size characteristic of lamnid embryos at this stage in their development. Evidence from this study suggests that adelphophagy does not occur in the porbeagle. The ova capsules observed in our study were similar to those found in the sandtiger and other lamnid sharks described by Gubanov (1972), Fujita (1981), Gruber and Compagno (1981), Gilmore et al. (1983), Francis and Stevens (2000), and Mollet et al. (2000).

Embryonic growth was estimated at 8.15 cm per month in our study (Fig. 10). Francis and Stevens (2000) estimated embryonic growth of approximately 7.48 cm per month for embryos in the South Pacific. New data from the South Pacific (Francis[7]) refined this estimate to 8.47 cm per month. Examination of more late-term embryos will further refine this estimate for the NW Atlantic.

Our results indicated a one year reproductive cycle, with gestation lasting 8–9 months. Mating occurs between September and December. Based on the one late-term female and several postpartum females it appears that parturition occurs from early April though June. Aasen (1963) estimated that parturition occurs from late May to early June in the NW Atlantic and suggested about an 8-month gestation period based on the lack of gravid female porbeagles from June to September. All females we examined in December were gravid. Although a nongravid mature portion of the female population could reside elsewhere, we have no data to support this and thus assume that porbeagle females reproduce annually. Parturition time and location and late embryonic development and growth rates need further investigation.

Mean litter size in the NW Atlantic was found to be 4.0—usually two embryos per uteri. Mean litter size from the SW Pacific Ocean was 3.8 from 138 embryos representing 43 litters (Francis and Stevens, 2000). Mean litter size from the NE Atlantic Ocean was 3.7 based on 12 litters examined by Gauld (1989). The sex ratio of the embryos examined in our study was 1:1, which agrees with the findings of Francis and Stevens (2000) for the SW Pacific Ocean. The smallest free-swimming porbeagles in the NMFS historical tagging database range in size from 55 to 79 cm FL (mean 71 cm FL)[7] from April to June; this length range, along with that of the one late-term litter (50–59 cm FL), suggests a birth size similar to Aasen's[4] (1963) prediction of 67 cm FL and to Francis and Steven's (2000) estimate of 58–67 cm FL for the SW Pacific. However, length at birth needs further analysis because few neonates were observed during the parturition period.

Acknowledgments

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Integration of submersible transect data and high-resolution multibeam sonar imagery for a habitat-based groundfish assessment of Heceta Bank, Oregon*

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Abstract—In the face of dramatic declines in groundfish populations and a lack of sufficient stock assessment information, a need has arisen for new methods of assessing groundfish populations. We describe the integration of seafloor transect data gathered by a manned submersible with high-resolution sonar imagery to produce a habitat-based stock assessment system for groundfish. The data sets used in this study were collected from Heceta Bank, Oregon, and were derived from 42 submersible dives (1988–90) and a multibeam sonar survey (1998). The submersible habitat survey investigated seafloor topography and groundfish abundance along 30-minute transects over six predetermined stations and found a statistical relationship between habitat variability and groundfish distribution and abundance. These transects were analyzed in a geographic information system (GIS) by using dynamic segmentation to display changes in habitat along the transects. We used the submersible data to extrapolate fish abundance within uniform habitat patches over broad areas of the bank by means of a habitat classification based on the sonar imagery. After applying a navigation correction to the submersible-based habitat segments, a good correlation with major boundaries on the backscatter and topographic boundaries on the imagery were apparent. Extrapolation of the extent of uniform habitats was made in the vicinity of the dive stations and a preliminary stock assessment of several species of demersal fish was calculated. Such a habitat-based approach will allow researchers to characterize marine communities over large areas of the seafloor.

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Dramatic declines in several groundfish populations have occurred along the U.S. West Coast during the last decade (Ralston, 1998; PFMC[1]; Sampson,[2] Bloeser[3]). One problem exacerbating these declines is that current stock assessments are not sufficiently precise or accurate to effect empirically based management. This is especially true for commercially important species of rockfish (Scorpaenidae, *Sebastes*), which comprise major groundfish fisheries along the Pacific Coast. Although evidence has accumulated for substantial declines in the abundance of several species of rockfish, the overall picture is unclear because 42 of 54 rockfish species (78%) have never been assessed (Ralston, 1998; NMFS, 1999; Bloeser[3]). Of the 12 species that have been assessed by the National Marine Fisheries Service, five were listed as "overfished" and one species was listed as "approaching overfished condition" (NMFS, 1999).

A possible alternative to single-species stock assessments of demersal fishes is a habitat-based community assessment, which serves to estimate groundfish population sizes by recognizing that species are not randomly distributed among varying habitats. It is known that the diversity, quality, and extent of bottom habitats are important in determining the distribution, abundance, and diversity of rockfishes (Carlson and Straty, 1981; Pearcy et al., 1989; Carr, 1991; Stein et al., 1992; O'Connell and Carlile, 1993). It has been previously demonstrated, within local study areas, that species richness and composition correlate with seafloor texture (Hallacher and Roberts, 1985; Richards, 1986; Love et al., 1991; Stein et al., 1992; Krieger, 1993; Yoklavich et

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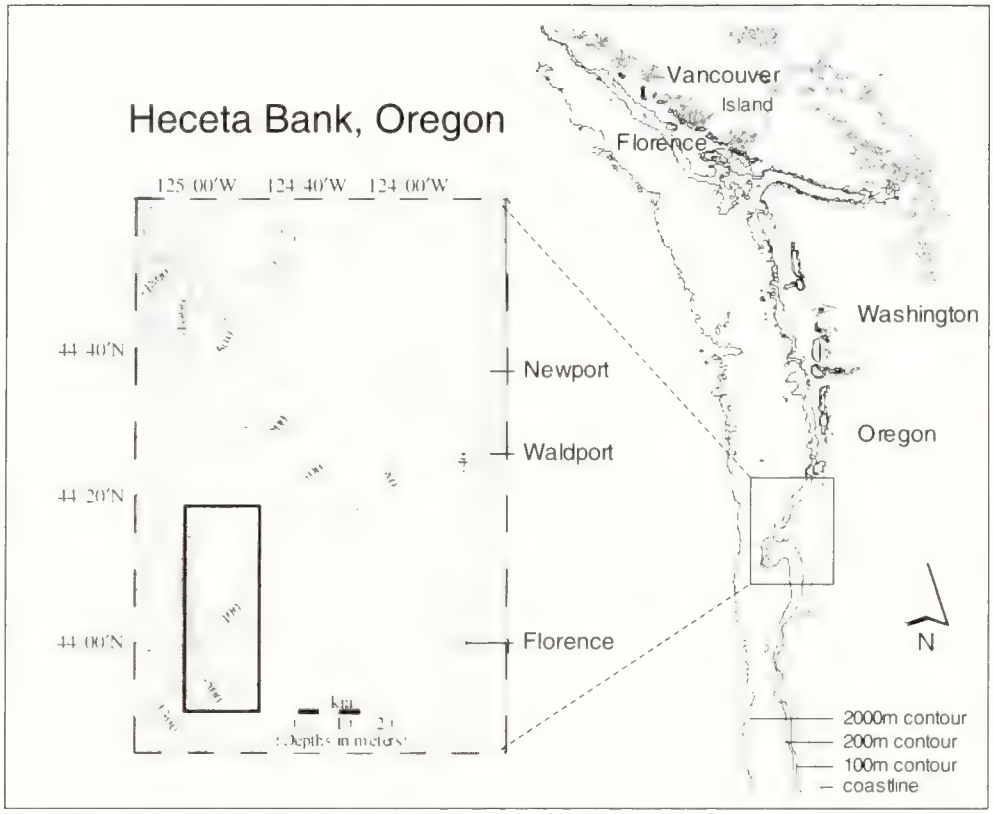

Figure 1

Location of Heceta Bank and the adjacent continental margin in relation to the Oregon coast. The survey area is outlined in bold lines.

al., 2000; Hixon et al.[4]; Hixon and Tissot[5]). Correlations over larger regions have been difficult to determine because of the limitations in the resolution and areal coverage of bathymetric charts, which are crucial in providing broad-scale habitat data. However, this difficulty no longer exists with the advent of differential GPS and high-resolution sonar systems (Hughes Clarke et al., 1996). When adequately groundtruthed, these new systems provide bathymetric and backscatter data with sufficient resolution to formulate habitat classifications over broad areas of the continental shelf and slope (Able et al., 1987; Yoklavich et al., 1995; Greene et al.[6]; Fox et al.[7]).

We developed this habitat-based groundfish assessment strategy by integrating a comprehensive submersible survey with new high-resolution sonar imagery of the seafloor. Sonar images produce habitat data by using acoustic signals to differentiate areas of hard substrata from surrounding soft sediments based on differences in the intensity of reflected sound. This technology has the distinct advantage of examining large regions of seafloor sediment and geological topographic features without relying on expensive direct underwater bottom sampling and observation techniques. Sonar data can be used in an assessment of seafloor habitat and fish density over large areas by extrapolating from direct observations of fish and seafloor morphology transects using manned submersibles or remotely operated vehicles.

The study site for this assessment was Heceta Bank, a 50-km long outcrop on the outer shelf of central Oregon (Fig. 1). Heceta Bank is the largest rocky reef of the Pacific Northwest and is characterized by high variability in bottom types and textures. The bank provides a diversity of habitat types for many species of groundfish and

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[5] Hixon, M. A., and B. N. Tissot. 1992. Fish assemblages of rocky banks of the Pacific northwest. Final report supplement, OCS Study MMS 92-0025, 128 p. USDI Mineral Management Service, 770 Pasea, Camarillo, CA 93010.

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[7] Fox, D., M. Amend, and A. Merems. 1999. Nearshore rocky reef assessment. Coastal Management Section 309 Grant. Contract No. 99-072. Oregon Department of Fish and Wildlife, 2040 SE Marine Science Drive, Newport, OR 97365

invertebrates. These characteristics have made Heceta Bank one of the largest and most important of the heavily fished rocky banks in the Pacific Northwest. Along with its commercial importance, the bank has been the subject of substantial scientific research, which has made it an ideal site for developing these methods.

Direct observations of Heceta Bank were first made in 1987 in a series of 16 submersible dives used to characterize fish populations and habitats on the bank (Pearcy et al., 1989). These initial dives were used to select representative transects which were repeated in 1988, 1989, and 1990 using the manned research submersible *Delta* (Hixon et al.[4]; Stein et al., 1992). The objective of these surveys was to investigate relationships between the abundance of groundfish and macroinvertebrates and the topography and texture of the seafloor, as well as to document interannual variation in these relationships. Fish observed during these surveys included 69 taxa, representing 24 families, dominated by 24 species of rockfish. Multivariate analysis detected statistical relationships between habitat characteristics and fish distribution and abundance by species and provided comprehensive data on fish-habitat associations, as well as a baseline for future comparisons.

Although invaluable, data from this set of submersible dives provided detailed "snapshots" of very limited areas of the Bank. To complement this study and to provide a broad view of the bank, a survey was performed in 1988 with hull-mounted, Simrad EM300 multibeam sonar, which provided high-resolution bathymetry and backscatter imagery of most of Heceta Bank (Merle et al.[8]).

Materials and methods

Submersible dives

Submersible observation data were collected by using the manned submersible *Delta* at six predetermined stations along Heceta Bank. Detailed descriptions of submersible operations used in our study can be found in Hixon et al.[4] and Stein et al. (1992), and a brief description follows. Surveys were conducted in the month of September and consisted of 18 dives in 1988, 12 in 1989, and 12 in 1990, for a total of 42 dives and 84 transects (Fig. 2). Each dive consisted of two 30-minute timed transects and a 10–15 minute "quiet period" between transects to assess the effects of the submersible's lights and motors on local fish distribution. The average length of each 30-minute transect was approximately 1015 m. Data on fish species, size, and abundance were collected by direct observations through the forward view port from approximately 2 m above the bottom, providing a bracketed transect width of about 2.3 m. During the transects, observations were verbally tape-recorded and visually recorded with a VHS

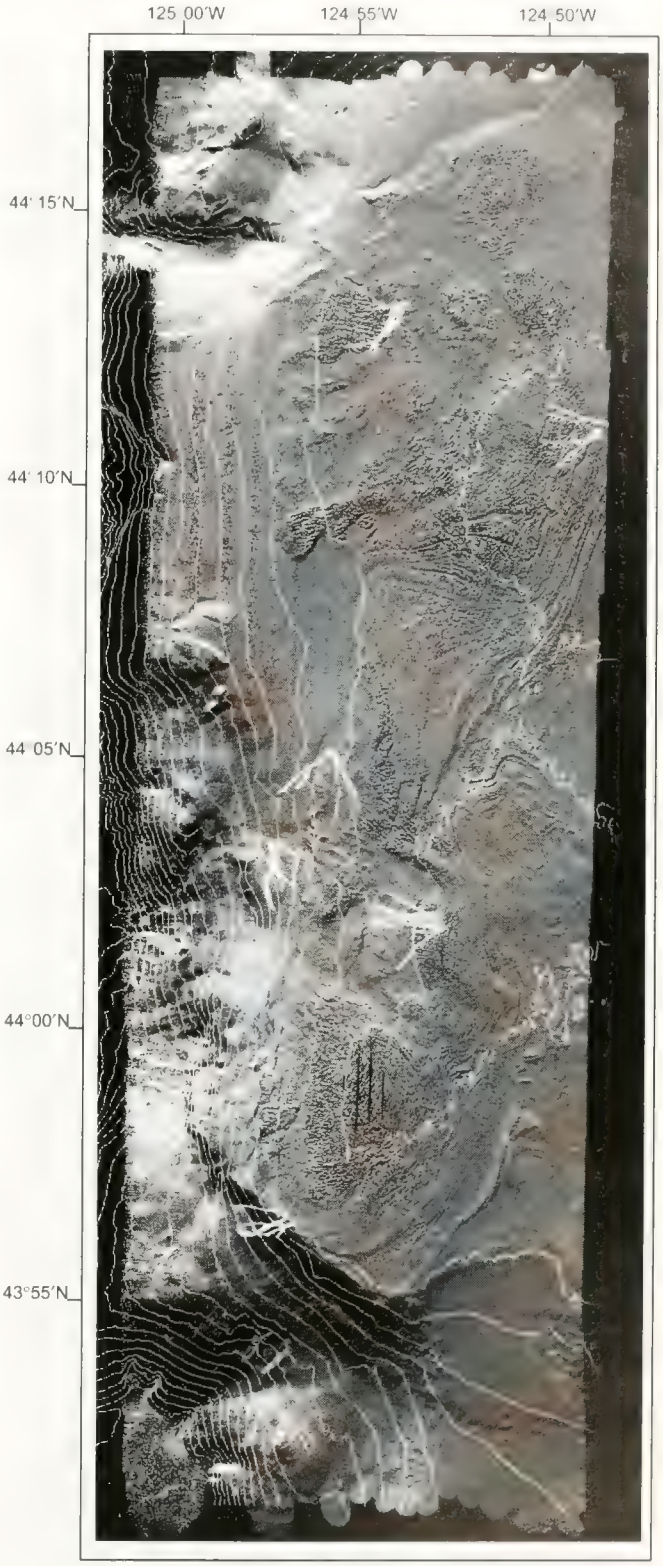

Figure 2

Simrad EM300 multibeam bathymetry illuminated from the northwest, which creates shadows to the southeast of the relief. The 1988, 1989, and 1990 *Delta* submersible transects (six clusters of white lines) have been overlaid on top of the bathymetric data. The isobathymetric contours are at 50-m intervals, beginning with 100 m on the east side of the bank.

[8] Merle, S., R. W. Embley, J. Reynolds, D. Clague, C. Goldfinger, and R. Yeats. 1998. A high-resolution image over the Heceta Bank off Central Oregon. Trans. Am. Geophys. Union 78, Fall Meeting Suppl., F818.

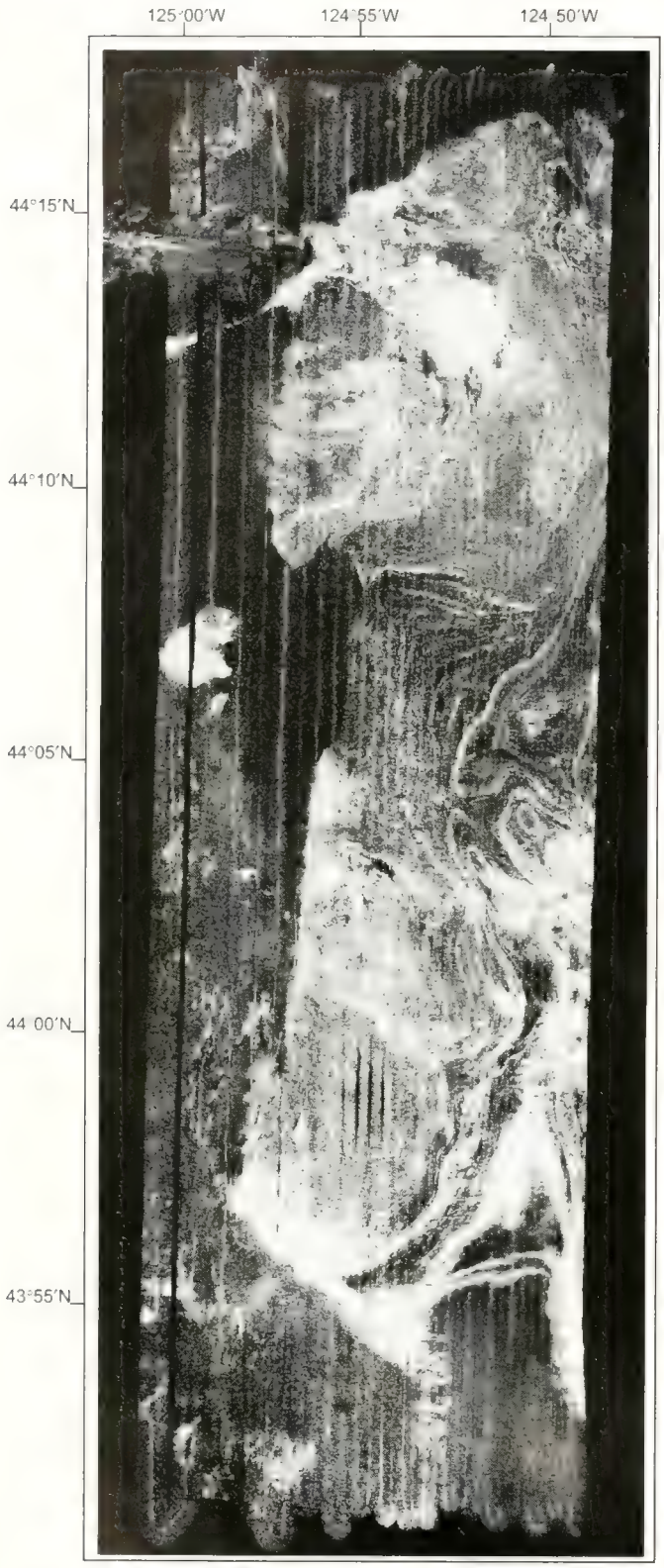

Figure 3

Backscatter imagery of Heceta Bank from Simrad EM300 multibeam survey. The lighter the shading the higher the reflectivity of the substratum.

videotape equipped with a timed data logger and audio track.

Direct and videotaped observations along the transects consisted of the number of species of fish and macroinvertebrates, and bottom-type characteristics. Fishes along the transects were identified, counted, and lengths were estimated to the nearest decimeter with a three-decimeter fiberglass rod suspended within the observer's view. Bottom type was categorized from videotapes by using a two-code combination, the first letter indicating the primary substratum (defined as covering at least 50% of the area viewed) and the second letter indicating the secondary substratum (defined as covering more than 20% of the area viewed). If the field of view was a single substratum, or the second most abundant substratum covered less than 20% of the field, the same letter was employed twice (e.g. MM for pure mud). The seven possible categories in order of increasing particle size or relief were mud (M), sand (S), pebble (P, diameter <6.5 cm), cobble (C, >6.5 and <25.5 cm), boulder (B, >25.5 cm), continuous flat rock (F, low vertical relief), and diagonal rock ridge (R, high vertical relief). The latitude and longitude positions of each transect were determined by using Loran-C with a Trackpoint II ultrashort baseline tracking system and by positioning the vessel directly above the submersible every 10 to 15 minutes. At least three position points were made per transect and the locations of bottom type and biological data were interpolated between these points. The absolute accuracy of the submersible's position, obtained by using Loran-C, was within about 150 to 500 m (Melton, 1986).

Multibeam sonar

The acoustic survey of Heceta Bank was conducted in May of 1998 with a Simrad EM300 (30 kHz) multibeam sonar system on the RV *Ocean Alert* (Merle et al.[8]). This survey provided a highly detailed, precisely navigated seafloor map of bathymetry and seafloor texture (Figs. 2 and 3). The data were processed with Swathed software (Hughes-Clarke et al., 1996). The data processing steps used in Swathed were the following: navigation and sounding editing, roll bias correction, tide correction, refraction correction, map sheet setup, gridding, and mosaicing which resulted in a composite map made up of acoustic backscatter imagery. The survey consisted of 47 overlapping north–south swaths up to 45 km long, which provided images of approximately 725 km^2 of the seafloor and nearly 100% coverage of high-resolution bathymetry and backscatter amplitude. These data were displayed in grids with a resolution of less than 5 meters on the shallowest portions of the bank from depths of 70 to 150 meters, and of about 5 to 10 meters at depths down to about 500 meters.

Data integration and habitat assessment

The sonar and submersible transect data were combined by using ArcView and ArcInfo geographic information system (GIS) software. The sonar data used were

bathymetry and backscatter and the submersible transect data included bottom type characteristics and fish density data. In order to represent the dive transects in GIS as linear features displaying changes in habitat and fish density, a dynamic segmentation data structure was used (ESRI, 1994).

Bottom type and fish density data to be displayed using dynamic segmentation were derived from transect observation data. Transects were divided into segments by uniform bottom type. Fish density was calculated along each segment of habitat type by using the data for the most common species observed, accounting for 90% of the total, plus a few rare species of commercial importance (i.e. lingcod, sablefish, Dover sole and rex sole). This complex of species consisted of a mixture of demersal and benthopelagic species. The following species were assessed: juvenile *Sebastes* sp. (unknown juvenile rockfish), *Sebastes chlorostictus* (greenstriped rockfish), *Sebastes wilsoni* (pygmy rockfish), *Sebastes helvomaculatus* (rosethorn rockfish), *Sebastes zacentrus* (sharpchin rockfish), *Sebastes flavidus* (yellowtail rockfish), *Ophiodon elongatus* (lingcod), *Sebastolobus alascanus* (shortspine thornyhead), *Anoplopoma fimbria* (sablefish), *Microstomus pacificus* (Dover sole), and *Errex zachirus* (rex sole). The density of fish (number per hectare) was calculated by taking the number of fish sighted in that habitat segment, dividing by the area of the habitat segment in meters, and multiplying by 10,000 square meters per hectare.

The use of dynamic segmentation data structure allowed for the display of changes in bottom type and fish density data within the transect lines. This was done by creating a "route" system in ArcInfo from the dive transect data and associating it with an "event table." The event table consisted of bottom type and fish density data, and their corresponding locations along the transect, and a route-identifier number to link the information to the corresponding transects in the route system. For visual display, bottom type segments were combined into three major habitat groups: 1) mud, which consisted of "MM" observations, 2) rock ridge, which consisted of "RR" observations, and 3) mixed substrate habitat, which consisted of combinations of all other bottom type observations.

In order to combine the sonar and submersible data sets, all segmented dive transect data were then reprojected with a 500-meter offset to the east. This was determined to be the best correction for discrepancies between the transect position data which were acquired by Loran-C and the sonar data which came from GPS positions. It was determined that this offset was necessary by comparing the two data sets and matching depth contours and borders of well-defined habitat, specifically interfaces between the mud and rock features of the bank. There did not appear to be a significant north–south offset, although this effect was more difficult to determine because the submersible transects did not cross any well-defined north–south boundaries. Transects segmented by both bottom type and fish density were overlaid on the sonar data in ArcView (Fig. 4, A–C).

Assessments of fish abundance within large habitat areas were performed by selecting patches of relative habitat homogeneity on the sonar map around the location of each submersible transect. These patches were chosen by examining both patterns in the backscatter values and topographic features indicated by the backscatter and bathymetric data. In areas of mud off the bank, borders were chosen by maintaining constant depth as well as equal distance from the bank. In selecting patches to represent areas of similar habitat, the boundaries were relatively well defined in areas of rock and mud, but for mixtures of sand, cobble, pebble, and boulder, it was more difficult to distinguish distinct boundaries and therefore these patch borders were drawn conservatively.

Using the observational data from the transects from all three years, we were able to characterize each habitat patch by percent bottom type, density of fish, and estimated abundance of fish as extrapolated from the dive transect data contained within that patch. The grand mean density and standard error for each species was determined by using a weighted density for each habitat segment based on a proportion of the length of that segment to the overall transect distance within that habitat patch. The grand mean density was calculated as

$$x = \sum_{i=1}^{n} d_i p_i, \tag{1}$$

where $x = \bar{x}$;

d = density of fish within a segment of continuous bottom type; and

p = bottom type segment length/total transect length within the patch.

This calculation used the associations of the fish species with substrate type and weighted its contribution to the overall density by the comparative length of that segment. Total fish abundance for each habitat patch was determined by multiplying the area of the patch and the grand mean density and standard error of each species. The total abundance for each species for all habitat patches was determined by adding the abundance for that species for all eight habitat patches. The standard error for the total abundance for each species was determined by calculating a grand mean standard error weighted by using the standard error of each habitat patch multiplied by the proportion of the abundance of that species for that habitat patch to the overall abundance for that species. Total abundance standard error was calculated by using Equation 1 where x = SE; d = standard error of fish abundance within a habitat patch; and p = abundance within that habitat patch/total abundance in all eight patches.

Results

Comparing the submersible data with the sonar data, we found that there was high correlation between the direct observations of bottom type and the habitat type indicated by the sonar data. Side-lit bathymetry revealed areas of outcropping substrata and the backscatter data

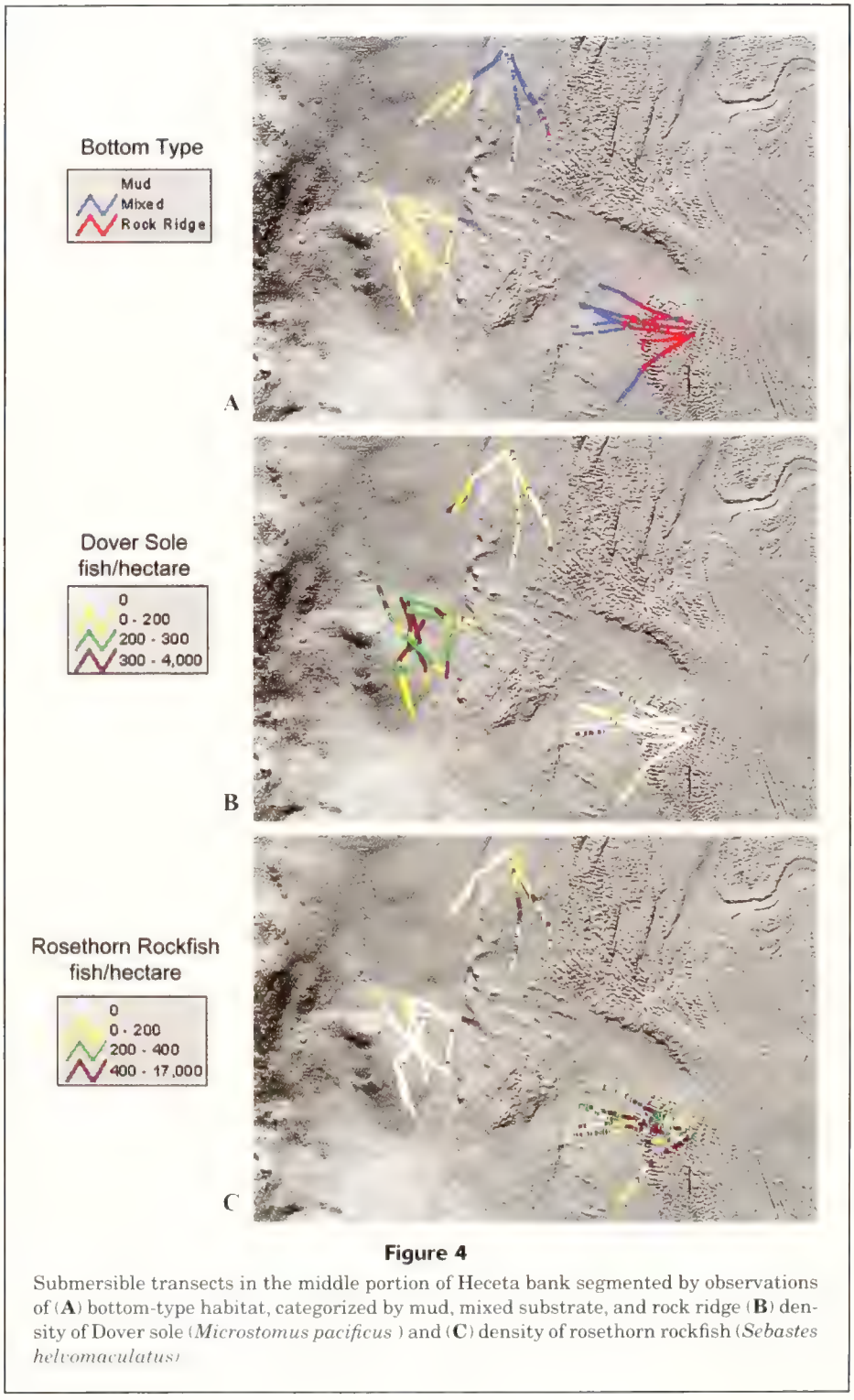

Figure 4

Submersible transects in the middle portion of Heceta bank segmented by observations of (**A**) bottom-type habitat, categorized by mud, mixed substrate, and rock ridge (**B**) density of Dover sole (*Microstomus pacificus*) and (**C**) density of rosethorn rockfish (*Sebastes helvomaculatus*)

showed changes in seafloor texture. Borders of rock ridge and mud observed in the submersible survey matched the bathymetric data, indicating areas of high relief for rocky patches and low relief for areas of mud (Figs. 4A and 5). Changes in backscatter also corresponded with changes observed in bottom type from the submersible data (Fig. 5).

It was noted consistently that high-backscatter areas were associated with mixed substrate habitat, comprising a combination of pebble, cobble, and boulder, which due to their size and geologic composition have a relatively high reflectivity. Mid-backscatter values were found to be associated with rock ridge features. These are typically

Figure 5

Habitat patch boundaries and transects segmented by bottom type overlaid on both bathymetric and backscatter sonar images. Habitat patches are labeled A–H. The bottom-type observations were grouped into three predominant habitats: mud, mixed substrate, and rock ridge.

large-scale rolling ridges with less small-scale relief. Low-backscatter values were associated with mud bottoms, which have characteristically low reflectivity.

Eight regional patch boundaries were drawn based on areas of relative homogeneous seafloor sonic characteristics around the six stations surveyed by submersible (Fig. 5). These patches (labeled A–H) ranged from 1.8 km^2 (patch B) to 38.9 km^2 (patch C) (Table 1). Patch boundaries for A, C, and F were drawn around areas of mid-backscatter reflectivity and high relief indicated by the bathymetric data, and were located in relatively shallow areas of the bank (75–125 m). Patch boundaries for D and H were drawn around mud areas located off the edge of the bank, which exhibited low-backscatter values, low relief on the bathymetric data, and were located in deeper waters (150–300 m). Patch boundaries for B, E, and G were drawn around areas of high backscatter and were present in intermediate depths (100–150 m).

Table 1

Estimated mean fish density and abundance (± standard error) by habitat patch (A–H) and species at Heceta Bank, Oregon. Density is in number of fish/hectare, abundance numbers are × 1000, and *n* = number of bottom type segments.

		Habitat patch								
		A	B	C	D	E	F	G	H	
	Habitat type	Rock ridge	Mixed	Rock ridge	Mud	Mixed	Rock ridge	Mixed	Mud	
	Area (km^2)	6.2	1.78	38.9	25.1	19.9	5.05	15.5	12.0	Total
Fish taxa	*n*	81	137	262	51	268	219	58	44	124
Juvenile rockfish	density	1140 ±536	1001 ±385	25,577 ±6521	2 ±1	95 ±217	4709 ±5309	30 ±12	0 ±0	
Sebastes sp.	abundance	711 ±335	178 ±69	99,595 ±25,394	6 ±3	190 ±433	2380 ±2683	46 ±18	0 ±0	103,110 ±24,593
Greenstriped rockfish	density	108 ±23	137 ±27	3 ±3	18 ± 13	232 ±23	10 ±4	65 ±23	0 ±0	
S. elongatus	abundance	68 ±15	24 ±5	13 ±10	46 ±32	463 ±46	5 ±2	101 ±35	0 ±0	759 ±37
Pygmy rockfish	density	2195 ±536	12,435 ±3392	3586 ±1264	0 ±0	2260 ±1139	12,119 ±3531	3236 ±581	0 ±0	
S. wilsoni	abundance	1370 ±335	2218 ±605	13,962 ±4922	0 ±0	4509 ±2273	6125 ±1785	5016 ±901	0 ±0	35,041 ±2746
Rosethorn rockfish	density	367 ±56	540 ±54	379 ±55	10 ± 24	238 ±21	473 ±121	595 ±88	5 ±2	
S. helvomaculatus	abundance	229 ±5	96 ±10	1478 ±213	24 ±61	475 ±43	239 ±61	922 ±137	6 ±2	3643 ±134
Sharpchin rockfish	density	265 ±71	1632 ±308	0 ±0	9 ±16	727 ±112	2 ±0.5	2916 ±505	0 ±0	
S. zacentrus	abundance	166 ±44	291 ±55	0 ±0	23 ±40	1450 ±224	1 ±0	4519 ±783	0 ±0	7552 ±515
Yellowtail rockfish	density	885 ±535	639 ±224	287 ±101	0 ±0	6 ±4	1578 ±421	0 ±0	0 ±0	
S. flavidus	abundance	552 ±334	114 ±40	1116 ±391	0 ±0	13 ±8	797 ±213	0 ±0	0 ±0	2747 ±289
Lingcod	density	2 ±5	4 ±5	27 ±5	0 ±0	3 ±2	23 ±70	9 ±3	0 ±0	
O. elongatus	abundance	1 ±3	1 ±1	103 ±19	0 ±0	6 ±3	12 ±35	14 ±4	0 ±0	143 ±17
Shortspine thornyhead	density	0 ±0	0 ±0	0 ±0	228 ±41	0 ±0	0 ±0	199 ±72	457 ±46	
S. alascanus	abundance	0 ±0	0 ±0	0 ±0	575 ±104	0 ±0	0 ±0	309 ±111	549 ±56	1433 ±87
Sablefish	density	0 ±0	0 ±0	0 ±0	52 ±10	0.7 ±0.6	0 ±0	23 ±25	96 ±35	
A. fimbria	abundance	0 ±0	0 ±0	0 ±0	131 ±25	1 ±1	0 ±0	36 ±39	116 ±42	284 ±34
Dover sole	density	28 ±20	41 ±17	0 ±0	312 ±33	79 ±14	8 ±5	137 ±71	217 ±29	
M. pacificus	abundance	17 ±12	7 ±3	0 ±0	786 ±82	158 ±29	4 ±3	212 ±110	260 ±35	1445 ±70
Rex sole	density	0 ±0	7 ±6	0 ±0	143 ±18	23 ±7	0 ±0	3 ±3	24 ±14	
E. zachirus	abundance	0 ±0	1 ±1	0 ±0	359 ±44	46 ±15	0 ±0	5 ±5	29 ±17	440 ±39
Total abundance		3115 ±288	2932 ±469	116,267 ±22,350	1949 ±28	7312 ±1464	9563 ±1830	11,181 ±738	960 ±47	156,598 ±16,854

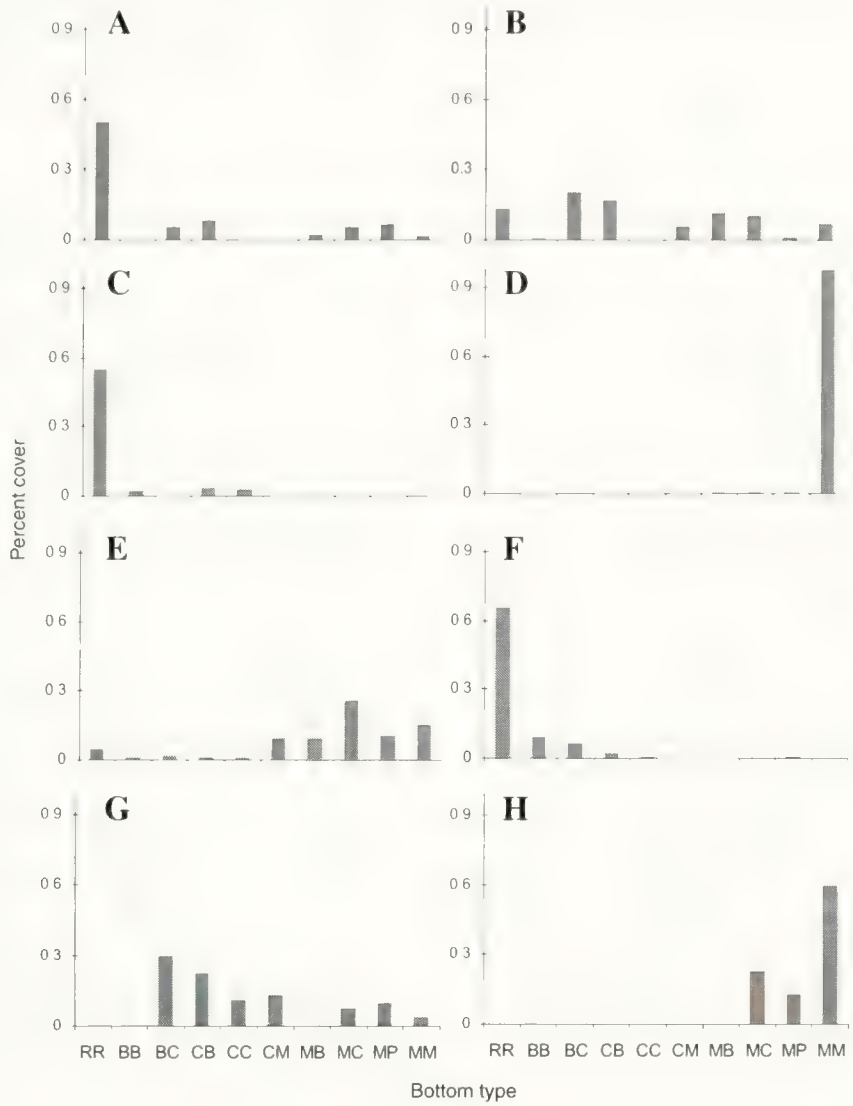

Figure 6

Percent cover of bottom types calculated from observations of all transects contained within each of the eight habitat patches labeled A–H. Bottom types are listed from left to right by decreasing relief and particle size, where the first letter is the dominant substratum and the second letter is the second most prevalent substratum. Substrate categories shown comprise only the 10 most dominant bottom types, consisting of combinations of R = rock ridge, B = boulder, C = cobble, M = mud, and P = pebble.

Combining the sonar-derived habitat patches and submersible observations gave an indication of bottom-type compositions for the defined patches. Of the eight habitat patches analyzed, three of the habitat patches were predominantly rock ridge (patch A—63% RR and 14% RC/RB; patch C—55% RR and 3% RB/RC; and patch F—66% RR), two were predominantly mud (patch D—98% MM; and patch H—60% MM and 36% MC/MP), and three were a mixture of boulder, cobble, pebble, and mud (patch B—75% BC/CB/MB/MC/MM/CM/MP/BM/BB; patch E—83% MC/MM/MP/CM/MB/CP/BM/BC/CB/PM/CC/BB/BP/PB; and patch G—100% BC/CB/CM/CC/MP/MC/MM/PM/BB) (Fig. 6).

There were differences in fish density within the patches between the three major habitat classification types, as well as differences among patches of similar bottom types (Fig. 7, Table 1). Species with the highest association with rock-ridge habitat patches were yellowtail rockfish, juvenile rockfish, and lingcod. Those primarily associated with mud habitats were Dover sole, rex sole, and shortspine thornyheads. Those associated with mixed substrate patches were sharpchin rockfish, rosethorn rockfish, green-

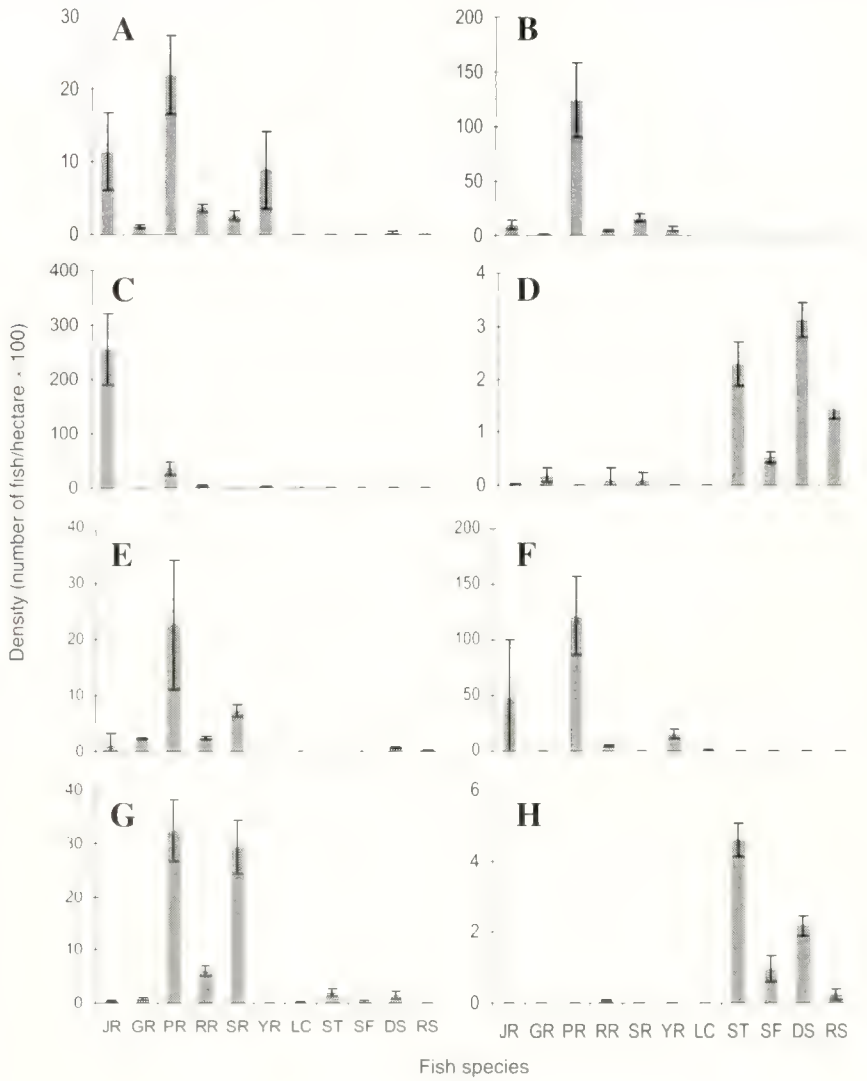

Figure 7

Fish densities (mean ±SE) for each habitat patch calculated from all transects contained within each patch. JR = juvenile rockfish (*Sebastes* species); GR = greenstriped rockfish (*Sebastes elongatus*); PR= pygmy rockfish (*Sebastes wilsoni*); RR = rosethorn rockfish (*Sebastes helvomaculatus*); SR = sharpchin rockfish (*Sebastes zacentrus*); YR = yellowtail rockfish (*Sebastes flavidus*); LC = lingcod (*Ophiodon elongatus*); ST = shortspine thornyhead (*Sebastolobus alascanus*); SB = sablefish (*Anoplopoma fimbria*); DS = Dover sole (*Microstomus pacificus*); and RS = rex sole (*E. zachirus*).

striped rockfish, and pygmy rockfish. Juvenile rockfish were found predominantly in rock-ridge habitats, and found in substantially high density (25,577 [±6521] fish/hectare) in patch C as compared with the other rock ridge patches (patch A 1140 [±536] fish/hectare and patch F 4709 [±5309] fish/hectare). Both Dover sole and rex sole were associated with mud habitat, and both were found in higher densities in patch D (Dover sole—312 [±33] fish/hectare, rex sole—143 [±18] fish/hectare) than patch H (Dover sol—217 [±29] fish/hectare, rex sole—24 [±14] fish/hectare). Pygmy rockfish were found in high density in mixed substrate patches B and F (12,435 [±3392] fish/hectare and 12,119 [±3531] fish/hectare) but at a substantially lower density in patch G (3236 [±81] fish/hectare).

Among all eight patches, the species found in the highest abundance overall were juvenile rockfish and pygmy rockfish, and those in the lowest abundance were lingcod and sablefish (Table 1). The total area of all habitats assessed was 124 km^2, which is approximately 17% of the total area of the sonar survey, and the total number of estimated fish and standard error for that area was 156,598,000 ±16,854,000. The coefficient of variation was relatively low

for greenstriped rockfish, rosethorn rockfish, sharpchin rockfish, shortspine thornyhead, and Dover sole (between 3.7% and 6%) and slightly higher for pygmy rockfish, yellowtail rockfish, lingcod, sablefish, and rex sole (between 7.8% and 11.9%).

Discussion

A primary finding of our study was that distinct bottom types found on Heceta Bank are distinguishable through the use of sonar data and that these interpreted habitats correlate with direct submersible observations of bottom type. The determination of habitat information from sonar data is significant in that it provides a broad-scale view of the seafloor habitat, previously unavailable, and allows a habitat-based groundfish assessment. Although seafloor imaging and GIS techniques have previously been used in the study of marine habitats (e.g. Meaden, 1999; McRea et al., 1999; Sherin, 1999; Yoklavich et al., 2000), ours is one of the first published studies where GIS technique was used to combine a detailed analysis of fish and habitat transect data with broad-area high-resolution sonar seafloor imagery and where total fish abundances were calculated for large areas of the seafloor (see also O'Connell et al.[9]).

Habitat type could not be determined by bathymetry or backscatter data alone, but the information provided by both data sets, in addition to groundtruthing by direct submersible observation, gives a clearer picture of the overall habitat environment. The use of the backscatter data combined with the bathymetric data has the advantage of providing an indication of substrate type, which is clearly important in fish-habitat associations. In general, however, backscatter provides a better indication of habitat for fish association purposes. Bathymetric data can provide geological structure on the resolution of five to ten meters, whereas backscatter data give an indication of structural variation on a smaller scale, which is of ecological importance in influencing the distribution of groundfish. For example, the physical properties of a substrate influence the types of invertebrates that colonize the seafloor, and local relief can provide microhabitats for some fish.

The extent to which a groundfish habitat can be effectively mapped by remote sensing is determined by the resolution of the system used. In general, sonars are optimized for specific operational depth ranges. A system designed for very shallow water can have sufficient resolution to provide contours of features or objects that deeper water (lower frequency and longer range) systems will only "see" as backscatter changes. As more sites are studied by combining visual seafloor transects, high-resolution sonar, and GIS techniques, it is likely the geologic indices most relevant to groundfish habitats will become apparent. These methods should lead to a more coherent approach to habitat-based stock assessments.

One of the limitations of this habitat-based approach to stock assessments has to do with strong reliance upon the fish-substratum association. The distribution and abundance of groundfish has been shown to be strongly correlated with substrate type (see introduction), but fish distributions and densities may vary with other factors as well, such as depth, currents, nutrients, and food availability. In this study there was an attempt to address this potential problem of over emphasizing the fish substratum relationship through the grouping of habitats into patches. The designation of habitat patches allowed the grouping of areas of potentially similar biotic and physical characteristics. Thus, the use of patches as areas for fish density estimates allowed for increased accuracy in forming abundance estimates from the habitat-groundfish association information. For example, this advantage was apparent by high variance in fish density estimates among patches of similar bottom type, such as the high density of juveniles in one of the three rock ridge patches. Variations in density in similar patch types of our study were also observed for Dover sole, rex sole, and pygmy rockfish. These patterns may be due to differences in depth, food availability or variations in percent composition of substrate type in separate areas of the bank. The other benefit of using habitat patches was that it allowed the testing of new groundfish assessment methods without making predictions for areas of high uncertainty where submersible transects were not performed.

Hixon et al.'s study[4] is one of only a few comprehensive habitat-groundfish studies available and has provided a foundation for testing this new approach. Hixon et al's dataset provided invaluable habitat information, but had several shortcomings. One problem was that of the inconsistency in positional data because of the use of Loran-C (GPS was not yet available). Another problem, characteristic of all submersible studies, was the overall limited spatial sampling provided by the survey. The stations for the study were chosen as representative habitats for Heceta Bank from exploratory submersible dives conducted by Pearcy et al. (1989) in 1987. However, not all of the representative habitat areas were sampled because maps of high-resolution bathymetry and backscatter were not available at that time. Lack of complete habitat data made it difficult to extrapolate bottom-type and fish-density data to the entire bank.

The use of observational data from submersibles for determination of fish density, and extrapolation from these data to total abundance within regional habitat patches, were based on several assumptions. First, we assumed that the areas sampled were representative of the entire regional patch to which each transect belonged. Whatever error was associated with this assumption, our approach is certainly more accurate that any method that ignores habitat variation. Second, we assumed that all fish within each submersible transect were accurately identified and counted. Identification of similar species of rockfish can be problematic, and counts clearly become estimates when dense schools are encountered. Third, we assumed

[9] O'Connell, V., and C. Carlile, and C. Brylinsky. 2001. Demersal shelf rockfish stock assessment and fishery evaluation report for 2002. Regional Information Report 1J01-35, 43 p. Southeast Region, Division of Commercial Fisheries, Alaska Department of Fish and Game, P.O. Box 25526, Juneau, AK 99802.

that avoidance or attraction of fish in response to the submersible was minimal, and thus did not affect counts substantially. This assumption was tested by Hixon et al.[4] by observing the local distribution and abundance of fish around the submersible just before and after the 10–15 minute "quiet periods" on the bottom, during which all motors and lights were turned-off. Quiet periods were conducted for all transect dives, and there was no indication that fish behavior was altered by the presence of the submersible. However, midwater schools of yellowtail rockfish sometimes circled the submersible during transects, which could have affected counts if fish were counted more than once. The final assumption was that transect width, which varied as a function of the altitude of the submersible above the seafloor, was constant. Certainly, there was some variation in altitude, yet the error introduced was presumably insubstantial except perhaps in areas of extremely heterogeneous vertical relief.

This study provides an expanded view of the groundfish habitat of Heceta Bank in areas adjacent to the historical *Delta* transects. In order to perform a full assessment of the bank it will be important to groundtruth habitat types for the entire extent of the bank. The new sonar data have indicated areas on the bank that contain unique habitats that have not been identified. The best study plan would have been to gather the sonar data first, then use the detailed imagery to define patches of uniform bottom type for planning subsequent stratified random sampling and groundtruthing using submersibles. The next phase of our project was initiated in June 2000 and involved operations with the manned submersible used in the original study and an advanced remotely operated vehicle (ROV) to conduct transects on unsurveyed areas, as well as to repeat the original historical transects. Not only will this approach optimize the techniques developed in our project but may also provide the opportunity to estimate changes in fish density on Heceta Bank over the past decade.

Conclusions

In this exploratory project we have demonstrated how sonar and submersible data can be combined to allow habitat-based stock assessments of multiple species of groundfish. Despite its limitations, this method provides the possibility for a detailed look at fish abundance using habitat associations. This approach could be used to address the problem of the high number of groundfish species that are currently unassessed. It offers the prospect of examining multiple species of fish and may provide a better indication of fish abundance estimates, particularly for multiple species, than is possible using current methods.

The method presented in our study provides an alternative for assessing these ten groundfish species and additional groundfish species that are currently unassessed, as well as for monitoring species that are considered to be overfished. Of the groundfish species examined in this study using the 1988–90 submersible observations, the status of all, but the pygmy, rockfish has been reported recently (NMFS, 1999). In the NMFS report on the status of fisheries in the United States, only the lingcod was reported as "overfished." Yellowtail rockfish, shortspine thornyhead, sablefish, and Dover sole were listed as "not approaching overfished," and the status of rex sole, greenstriped rockfish, rosethorn rockfish and sharpchin rockfish was reported as "unknown" (NMFS, 1999). In addition to the ten species that were examined here, the method described in our study would be important for assessing species of rockfish found on Heceta Bank that are considered overfished, such as the canary rockfish, Pacific ocean perch, and darkblotched rockfish. It should be stressed, however, that this method would be useful only for those species that are closely associated with seafloor habitats and spend most of their time near the bottom. For example, yellowtail rockfish are found as high as 25–35 m off the seafloor, so that transect data collected on the seafloor may not accurately reflect their true abundance (Pearcy, 1992).

The preliminary work in this study is a step toward creating a model approach for characterizing and quantifying groundfish and their habitat associations on a scale meaningful to the stock assessment of commercial species and the conservation of benthic communities. Traditional stock assessment methods for groundfish have been inadequate. Our study is the first step in the development of a new quantitative method of assessing groundfish stocks that is independent of traditional trawl surveys. Overall, this habitat-based approach to stock assessment has particular recommendation for defining and mapping essential fish habitat, as well as providing important data for designing and managing marine reserves and protected areas.

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An examination of spatial and temporal genetic variation in walleye pollock (*Theragra chalcogramma*) using allozyme, mitochondrial DNA, and microsatellite data*

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Abstract—We used allozyme, microsatellite, and mitochondrial DNA (mtDNA) data to test for spatial and interannual genetic diversity in walleye pollock (*Theragra chalcogramma*) from six spawning aggregations representing three geographic regions: Gulf of Alaska, eastern Bering Sea, and eastern Kamchatka. Interpopulation genetic diversity was evident primarily from the mtDNA and two allozyme loci (*SOD-2**, *MPI**). Permutation tests indicated that F_{ST} values for most allozyme and microsatellite loci were not significantly greater than zero. The microsatellite results suggested that high locus polymorphism may not be a reliable indicator of power for detecting population differentiation in walleye pollock. The fact that mtDNA revealed population structure and most nuclear loci did not suggests that the effective size of most walleye pollock populations is large (genetic drift is weak) and migration is a relatively strong homogenizing force. The allozymes and mtDNA provided mostly concordant estimates of patterns of spatial genetic variation. These data showed significant genetic variation between North American and Asian populations. In addition, two spawning aggregations in the Gulf of Alaska, in Prince William Sound, and off Middleton Island, appeared genetically distinct from walleye pollock spawning in the Shelikof Strait and may merit management as a distinct stock. Finally, we found evidence of interannual genetic variation in two of three North American spawning aggregations, similar in magnitude to the spatial variation among North American walleye pollock. We suggest that interannual genetic variation in walleye pollock may be indicative of one or more of the following factors: highly variable reproductive success, adult philopatry, source-sink metapopulation structure, and intraannual variation (days) in spawning timing among genetically distinct but spatially identical spawning aggregates.

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Detecting spatial structure in the genetic variation of some marine fishes is challenging because populations are often closely related due to high gene flow, and the relationships between populations may change over years (Hedgecock, 1994; Shaklee and Bentzen, 1998; Waples, 1998). For these species, independent population studies of genetic variation may result in conflicting evidence on the extent and complexity of population structure (McQuinn, 1997; Shaklee and Bentzen, 1998). Interpreting these results may be further complicated if the loci and classes of genetic markers differ by study and year. In addition, the discordant patterns of population structure may reflect complex population biology and ecology or merely differences in the resolving power of loci and marker classes to detect spatial structure. The walleye pollock (*Theragra chalcogramma*) is a marine fish that typifies this situation.

Walleye pollock inhabit basin, slope, and shelf waters of four major seas in the North Pacific Ocean: Sea of Japan, Sea of Okhotsk, Bering Sea, and Gulf of Alaska (Bailey et al., 1997). Their abundance is greatest in the eastern Bering Sea and the Sea of Okhotsk, but large aggregations are also found in the Sea of Japan, western Bering Sea, and the Gulf of Alaska. Smaller aggregations occur along coastal waters in bays and fjords such as in Prince William Sound, Alaska, and Puget Sound in Washington State. Population boundaries for walleye pollock may be correlated with the margins of spatially distinct spawning aggregates that occur throughout the species range in predictable locations during late winter and early spring (Bailey et al., 1999). Many of these spawning aggregates can be distinguished by spawning time and habitat, and by meristic and morphometric characters (e.g. Iwata, 1975b; Hinckley, 1987; Mulligan et al., 1989). Nevertheless, genetic support for discrete populations is equivocal, and the extent of population structuring in walleye pollock remains a controversial and unresolved issue for management and conservation in U.S. and international waters (Bailey et al., 1999).

Independent attempts to define genetic population structure in walleye pollock on a regional scale have shown mixed results. Some allozyme loci show genetic differentiation between walleye pollock from contiguous sea basins (e.g. eastern Bering Sea and Gulf of Alaska; Grant and Utter, 1980), and a single locus (*SOD*) appears to reveal a major east–west division between Asian and North American populations (Iwata, 1975a, 1975b; Grant and Utter, 1980). This major division is supported by a

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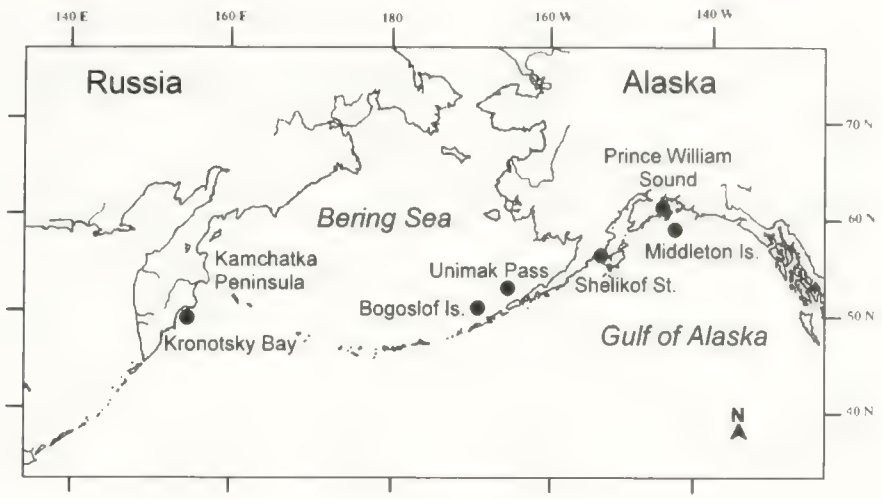

Figure 1

Map of the Gulf of Alaska and Bering Sea showing the location of walleye pollock spawning aggregations sampled for this study.

single study of mitochondrial DNA (mtDNA) sequence variation (Shields and Gust, 1995), but it is not evident in an unpublished study of microsatellite variation at two loci (reviewed in Bailey et al., 1999). Conversely, genetic differentiation among eastern Bering Sea and Gulf of Alaska populations is supported by the microsatellite study but is not supported by a study of mtDNA-RFLP (restriction fragment length polymorphism) variation (Mulligan et al., 1992). These discordant results may reflect attributes of walleye pollock population biology, the unique evolutionary properties of each marker class, or both. Nevertheless, an interpretation of the collective data is not possible because the studies were conducted as much as 22 years apart, and many samples were not from spawning aggregations.

Nonrepresentative sampling may bias attempts to define genetic population structure in walleye pollock, particularly on a fine spatial scale (within sea basins). For example, some studies using allozymes (Grant and Utter, 1980) and mtDNA (Shields and Gust, 1995) have included population samples taken during summer and fall, even though walleye pollock aggregate for spawning in late winter and early spring. These samples may obscure genetic differentiation because walleye pollock populations are believed to mingle in summer and fall during feeding migrations (Bailey et al., 1999). Also, the sample size used in some studies may be inadequate to detect population structure. The sample size in walleye pollock studies thus far has been typically less than 50, and the minimum sample size has been 22 (e.g. Grant and Utter, 1980; Mulligan et al., 1992). Sample sizes in this range (22–50) are generally insufficient to detect statistically significant differences in allele frequencies between populations that exhibit weak population structure (e.g. F_{ST} <0.02; Goudet et al., 1996; Ruzzante, 1998; Waples, 1998). These studies suggest that a sample size of 50 should be considered an absolute minimum for high gene flow species and that sample sizes of 100 or greater may be necessary when allele frequencies differ by 5% or less.

In our empirical study, we accounted for the sources of sample bias described above and addressed two important questions: 1) Do allozymes, mtDNA, and microsatellites provide concordant estimates of inter- and intraregional population structure in walleye pollock? 2) Is the genetic variation in walleye pollock populations stable from year to year? We tested for spatial patterns of genetic variation among six population samples from three regions: Gulf of Alaska, eastern Bering Sea, and eastern Kamchatka. We also tested for interannual stability of the genetic signal in replicate samples from three of the North American populations. Our results showed that two of 24 polymorphic allozyme loci (*SOD-2**, *MPI**) reveal significant spatial heterogeneity at the inter- and intraregional level. In general, the mtDNA data were concordant with these two allozymes, revealing significant genetic variation between North American and Asian (eastern Kamchatka) populations, as well as evidence of intraregional genetic variation, particularly among the Gulf of Alaska populations. The microsatellites, although highly polymorphic, showed little spatial variation. The allozyme and mtDNA data provided evidence of interannual genetic variation in two North American populations. F_{ST} values showed this interannual variation is of similar magnitude to the spatial variation in these populations.

Materials and methods

Sample collection

Tissue samples for allozyme and DNA analysis were obtained from six spawning aggregations of walleye pollock representing three major geographic regions: Gulf of Alaska, eastern Bering Sea, eastern Kamchatka (Fig. 1, Table 1).

Table 1

Location, sample data, and spawning habitat of walleye pollock examined in this study.

Major region and population	Spawning habitat	Date	*n*	N Lat.	W Long.
North America–Gulf of Alaska					
Shelikof Strait	shelf	1 Mar 97	100	57°55′	154°35′
		19 Mar 98	100	57°55′	154°40′
Prince William Sound	fjord	6 Feb 97	100	60°05′	148°20′
		6 Feb 98	100	60°05′	148°19′
Middleton Island	shelf	5 Mar 98	100	59°26′	145°45′
North America–Bering Sea					
Bogoslof Island	basin	1 Mar 97	100	53°15′	169°00′
		7 Mar 98	100	53°08′	169°11′
Unimak Pass	shelf	11 Apr 98	40	54°33′	165°38′
Asia–eastern Kamchatka					
Kronotsky Bay	shelf	1 Feb 99	96	52°00′	161°00′E

In total, nine samples were collected from 1977 through 1999: six from each of the major spawning aggregations shown in Figure 1, and three samples that were interannual replicates from Prince William Sound (PWS), Shelikof Strait (SHEL), and Bogoslof Island (BOG). Other samples included Unimak Pass (UNI) and Middleton Island (MID) in 1998 and Kronotsky Bay (KRON) in 1999. Tissue samples from heart, liver, muscle, and eye were taken from 100 individuals per population with the exception of Unimak Pass (n=40) and Kronotsky Bay (n=96). Only muscle tissue was sampled from Bogoslof Island walleye pollock in 1997. Samples were stored at –80°C until analyzed.

Allozyme analysis

Allozyme alleles were resolved by using horizontal starch-gel electrophoresis and enzyme-specific histochemical staining procedures described by Aebersold et al. (1987). Thirty six loci were screened for polymorphism (Table 2): *sAAT-1**, *sAAT-2**, *mAAT-1**, *ADA-1**, *ADA-2**, *AH-1**, *AH-2**, *ALAT**, *CK-A**, *FH**, *GAPDH-1**, *G3PDH-1**, *G3PDH-2**, *G3PDH-3**, *G3PDH-4**, *GPI-1**, *GPI-2**, *IDHP-1**, *IDHP-2**, *IDHP-3**, *LDH-2**, *LDH-3**, *MDH-A**, *MEP-1**, *MEP-2**, *MPI**, *PEPA**, *PEPB**, *PEPD**, *PEPLT**, *PGDH**, *PGM-1**, *PGM-2**, *SOD-1**, *SOD-2**, and *TPI**. Twenty-four loci were polymorphic in at least one of nine populations, and these loci were used in the tests of spatial and temporal genetic variation (Table 3).

DNA analysis

Total genomic DNA was isolated from 20–30 mg of heart tissue by using a Gentra Systems™ (Minneapolis, MN) Puregene DNA isolation kit. Precipitated DNA was hydrated in 50–100 µL tris-ethylenediaminetetraacetic acid (EDTA) buffer (10 mM Tris, 0.1 mM EDTA, pH 8.0) and heated at 55°C for approximately 12 h. Approximately 1 µL of hydrated DNA was used from each sample for polymerase chain reaction (PCR) amplification of mtDNA and microsatellite fragments.

mtDNA For an initial screen, six segments of the walleye pollock mitochondrial genome were examined for restriction fragment length polymorphism in a sample of 12 walleye pollock. The mtDNA segments examined were ND5/6 (~2400 base pairs /bp/; Cronin et al., 1993), cytochrome *b* (~1200 bp and~800 bp; Bickham et al., 1995), cytochrome oxidase I (~700 bp; Powers[1]), D-loop (~1400 bp; Cronin et al., 1993), and 16S (~600 bp; Palumbi et al., 1991). We used the following restriction enzymes: *Alu* I, *Apa* I, *Ase* I, *Ava* I, *Ava* II, *BamH* I, *Bcl* I, *Bgl* I, *Bgl* II, *BstE* II, *BstU* I, *Dpn* II, *EcoR* I, *EcoR* V, *Hae* II, *Hae* III, *Hha* I, *Hinf* I, *Hind* III, *Kpn* I, *Mse* I, *Msp* I, *Nci* I, *Pst* I, *Rsa* I, *Sac* I, *Sac* II, *Sau96* I, *Sca* I, *Stu* I, *Taq* I, *Xba* I, and Xho I.

PCRs were performed in 25–100 µL volumes containing 10 mM Tris-HCl (pH 8.3), 50 mM KCl, 2.0–3.5 mM $MgCl_2$, 0.8 mM dNTPs, 0.05 units/µL *Taq* polymerase, 0.3–1.2 µM primer, and about 250 ng DNA template. The PCR profile was 92°C (2 min) + 30–40 cycles of (92°C (30 sec) + *X*°C (30 sec) + 72°C (140 sec)) + 72°C (5 min), where the annealing temperature *X* varied among primer pairs. Restriction digests followed manufacturer's specifications (New England Biolabs, Beverly, Maine).

The mtDNA fragment and enzyme combinations ND5/6 (~2400 bp)—*Ase* I, *Ava* I, *Msp* I, *Rsa* I; cytochrome *b* (~1200 bp)—*Alu* I, *Hae* III, *Mse* I; and cytochrome oxidase (~700 bp)—*Alu* I revealed polymorphism and were used to test for spatial and temporal genetic variation. The PCR annealing temperatures for these fragments were the following: (for ND5/6) 50°C; (for cytochrome *b*) 54°C; and (for cytochrome oxidase) 50°C. Restriction fragments

[1] Powers, D. A. 1997. The use of molecular techniques to dissect the genetic architecture of pollock populations. Unpubl. rep. to the National Marine Fisheries Service, 11 p. Hopkins Marine Station, Stanford University, Pacific Grove, CA, 93950.

Table 2

Buffers and tissues used to resolve enzyme-coding loci in walleye pollock. Enzyme nomenclature and Enzyme Commission (EC) number follow IUBNC (1984); locus nomenclature follows Shaklee et al., (1990).

Enzyme or protein	EC number	Locus	Tissue[1] (buffer[2])
Aspartate aminotransferase	2.6.1.1	*sAAT-1**	L(AC6.5)
		*sAAT-2**	H(AC6.1), M(AC6.1)
		*mAAT-1**	M(AC6.1)
Adenosine deaminase	3.5.4.4	*ADA-1**	L(AC6.5)
		*ADA-2**	L(AC6.5)
Aconitate hydratase	4.2.1.3	*AH-1**	L(AC6.5)
		*AH-2**	H(AC6.5), M(AC6.1, AC6.5), L(AC6.5)
Alanine aminotransferase	2.6.1.2	*ALAT**	M(TBE)
Creatine kinase	2.7.3.2	*CK-A**	M(TBE)
Fumarate hydratase	4.2.1.2	*FH**	M(ACEN7.0)
Glyceraldehyde-3-phosphate dehydrogenase	1.2.1.12	*GAPDH-1**	M(AC6.9)
Glycerol-3-phosphate dehydrogenase	1.1.1.8	*G3PDH-1**	L(AC6.5)
		*G3PDH-2**	M(AC6.5), L(AC6.5)
		*G3PDH-3**	H(AC6.5), L(AC6.5)
		*G3PDH-4**	L(AC6.5)
Glucose-6-phosphate isomerase	5.3.1.9	*GPI-1**	H(TBCL)
		*GPI-2**	H(TBCL)
Isocitrate dehydrogenase (NADP+)	1.1.1.42	*IDHP-1**	L(ACE7.0), L(TC7.0)
		*IDHP-2**	M(ACEN7.0)
		*IDHP-3**	L(ACE7.0)
L-Lactate dehydrogenase	1.1.1.27	*LDH-2**	H(TBCL), M(TBE)
		*LDH-3**	H(TBCL), M(TBE)
Malate dehydrogenase	1.1.1.37	*MDH-A**	H(AC6.1), M(AC6.1, AC6.9)
Malic enzyme (NADP+)	1.1.1.40	*MEP-1**	M(AC6.5, AC6.9, ACEN7.0)
		*MEP-2**	M(AC6.5, AC6.9, ACEN7.0)
Mannose-6-phosphate isomerase	5.3.1.8	*MPI**	H(TBCL), M(TBE)
Dipeptidase	3.4.-.-	*PEPA**	H(AC6.5)
Tripeptide aminopeptidase	3.4.-.-	*PEPB**	M(AC6.9)
Proline dipeptidase	3.4.13.9	*PEPD**	M(AC6.1)
Peptidase-LT	3.4.-.-	*PEPLT**	H(AC6.1)
Phosphogluconate dehydrogenase	1.1.1.44	*PGDH**	M(AC6.9, ACEN7.0)
Phosphoglucomutase	5.4.2.2	*PGM-1**	H(TBCL), M(TBE), L(ACE7.0)
		*PGM-2**	M(TBE)
Superoxide dismutase	1.15.1.1	*SOD-1**	M(ACEN7.0, TBE)
		*SOD-2**	H(ACEN7.0)
Triose-phosphate isomerase	5.3.1.1	*TPI**	H(AC6.1), M(AC6.1)

[1] H = heart; E = eye; M = muscle; L = liver.

[2] Buffers: AC, ACN, ACE, ACEN: amine-citric acid buffer (Clayton and Tretiak, 1972) modified with EDTA (E), NAD (N), or both (Aebersold et al., 1987), values indicate pH; TBCL: tris-citric acid gel, pH 8.7 and lithium hydroxide-boric acid electrode buffer, pH 8.0 (Ridgway et al., 1970); TBE: tris-boric acid-EDTA buffer, pH 8.7 (Boyer et al., 1963).

were size fractionated on 3% agarose gels, stained with ethidium bromide, and visualized and photographed under ultraviolet light (312 nm). Fragment sizes as small as 50 bp were estimated by comparison with 100 bp and 250 bp ladders on each gel. A composite haplotype was generated for each individual by recording the presence or absence of restriction sites for all restriction enzymes and mtDNA segments (Lansman et al., 1981). The length of

Table 3

Single locus statistics: number of individuals (n); number of alleles (A); frequency of the most common allele over all populations (P_a); total heterozygosity (H_T); analogs of Wright's F-statistics F_{IS}, F_{ST}, and F_{IT} (f, θ, F). Note: The analog of F_{ST} for haplotype data, Φ_{ST}, is computed for mtDNA. Values in bold type with an asterisk are statistically significant. The α-level (0.05) was adjusted (α/k) for k tests, where k is the number of loci (allozymes, 24; microsatellites, 3).

Locus	n	A	P_a	H_T	f	θ	F
Allozyme							
*sAAT-1**	692	3	0.996	0.008	–0.001	–0.001	–0.003
*sAAT-2**	793	4	0.992	0.016	–0.011	0.006	–0.005
*mAAT-1**	803	2	0.998	0.004	0.001	–0.002	–0.001
AH-1	657	4	0.958	0.081	0.060	0.001	0.061
ALAT	811	3	0.898	0.188	–0.019	0.002	–0.017
*FH**	814	2	0.999	0.002	0.001	–0.001	–0.001
*G3PDH-2**	811	4	0.994	0.012	–0.002	–0.002	–0.004
*G3PDH-3**	715	4	0.992	0.016	–0.004	–0.002	–0.007
GPI 1	815	3	0.992	0.016	–0.008	0.002	–0.006
GPI 2	815	4	0.990	0.020	–0.010	0.003	–0.007
*IDHP-1**	714	4	0.976	0.047	–0.018	–0.001	–0.020
*IDHP-2**	814	3	0.996	0.008	–0.002	–0.001	–0.003
*LDH-2**	815	2	0.999	0.002	0.001	–0.001	–0.001
*LDH-3**	814	2	0.999	0.002	0.000	0.000	0.000
*MDH-A**	815	3	0.996	0.008	–0.002	0.000	–0.002
*MEP-1**	815	4	0.994	0.012	–0.004	–0.001	–0.004
*MPI**	810	5	0.788	0.337	0.016	**0.017***	0.032
PEPB[†]	802	4	0.962	0.074	–0.001	0.003	0.003
*PEPD**	815	3	0.985	0.030	**0.158***	–0.001	0.157
PGDH[†]	814	9	0.544	0.590	0.043	–0.002	0.041
*PGM-1**	815	4	0.993	0.014	–0.004	0.000	–0.004
*SOD-1**	815	2	0.999	0.002	0.000	–0.001	0.000
*SOD-2**	711	3	0.916	0.154	–0.014	**0.088***	0.075
TPI[†]	815	3	0.997	0.006	–0.002	0.000	–0.002
Mean	788	4	0.956	0.069	0.024	**0.010***	0.033
SE		1	0.100	0.136	0.014	0.011	0.010
Microsatellite							
Tch10	741	32	0.395	0.811	0.069	0.001	0.070
Tch12	671	12	0.305	0.782	0.035	0.000	0.035
Tch22	637	15	0.367	0.713	0.039	**0.005***	0.043
Mean	683	20	0.356	0.769	**0.048***	**0.002***	0.050
SE		11	0.046	0.050	0.011	0.001	0.011
mtDNA							
ND5/6-CB-CO	684	66	0.371	0.837		**0.022***	

the recognition sequence (bp) and the number of recognition sites identified by each enzyme were the following: for ND5/6—*Ase* I (6, 5), *Ava* I (6, 4), *Msp* I (4, 4), *Rsa* I (4, 5); for cytochrome *b*—*Alu* I (4, 2), *Hae* III (4, 2), *Mse* I (4, 7); and for cytochrome oxidase—*Alu* I (4, 4). A total of 150 nucleotides were surveyed for polymorphism or approximately 3.5% of the combined 4300-bp region.

Microsatellites Thirteen microsatellite loci were screened for polymorphism, amplification quality, and null alleles in walleye pollock by using primer pairs derived from Atlantic cod, *Gadus morhua*, (*Gmo1*, *Gmo2*, *Gmo9*, *Gmo10*, *Gmo123*, *Gmo132*, and *Gmo145*; Brooker et al., 1994) and walleye pollock (*Tch5*, *Tch10*, *Tch11*, *Tch12*, *Tch18*, and *Tch22*; O'Reilly et al., 2000). PCRs were performed in 10 µL volumes containing 10 mM Tris-HCl (pH 8.3), 50 mM KCl, 1.5 mM $MgCl_2$, 0.8 mM dNTPs, 0.05 units/µL Taq polymerase, 0.3–1.2 µM primer, and about 250 ng DNA template. The following PCR profile was used: 92°C (2 min) + 30 cycles of (92°C (30 sec) + X°C (30 sec) + 72°C (140 sec)) + 72°C (5 min) where the annealing temperature X varied among microsatellites.

Microsatellites were size fractionated by using an Applied Biosystems Inc. (ABI, Foster City, CA) 377-96 automated DNA sequencer operated in GeneScan™ mode (ABI, 1996a). Data were analyzed by using the internal

lane sizing standard and local Southern sizing algorithm in the GeneScan 672 software vers. 1.1 (ABI, 1996a). Alleles for each locus were scored and data were tabulated for importing into statistical software with Genotyper software, vers. 2.0 (ABI, 1996b).

Of the thirteen loci screened, *Tch10*, *Tch12*, and *Tch22* were used to test for spatial and temporal genetic variation. The PCR annealing temperatures for these loci were the following: (for *Tch10*) 54°C; (for *Tch12*) 47°C; and (for *Tch22*) 52°C. The loci *Gmo10*, *Gmo123*, *Gmo145*, *Tch5*, and *Tch18* did not amplify consistently by the methods above, and *Gmo1*, *Gmo2*, *Gmo9*, *Gmo132*, and *Tch11* appeared to possess null alleles as revealed by significant heterozygote deficits (data not shown).

Statistical analyses

Estimates of allele and haplotype frequency were calculated for each locus and population sample. Heterozygosity estimates (H) were calculated by using Equation 8.4 of Nei (1987) and haplotype diversity estimates (h) were computed by using the program ARLEQUIN vers. 1.1 (Schneider et al., 2000). A permutation test of the statistic $\hat{f}$ (Weir and Cockerham, 1984) was used to assess conformity to Hardy-Weinberg equilibrium (HWE) for each locus and over all loci for each population with the computer program FSTAT vers. 2.8 (Goudet 2000). The data set was permuted 1000 times (alleles were permuted among individuals, within population samples), and the threshold for statistical significance (α=0.05) was corrected for simultaneous tests by using the sequential Bonferroni method (Rice, 1989).

Spatial and temporal genetic variation were quantified by estimating analogs of Wright's F_{ST} for each marker class: θ (allozymes and microsatellites, Weir and Cockerham, 1984), R_{ST} (microsatellites, Slatkin, 1995), Φ_{ST} (mtDNA, Excoffier et al., 1992). Estimates of θ, R_{ST}, and Φ_{ST} ($\hat{\theta}$, $\hat{R}_{ST}$, and $\hat{\Phi}_{ST}$) were computed for all nine population samples, for all contemporaneous population samples (1997, 1998), and for the temporal replicates. The haplotype frequency estimates were used to compute Φ_{ST}. A hierarchical approach was used to determine if more detailed assessment of spatial variation was necessary. That is, only those statistics ($\hat{\theta}$, $\hat{R}_{ST}$, $\hat{\Phi}_{ST}$) that were significant over all samples from a given year were then calculated for populations pooled by region, and for populations within regions. Statistics significant at the regional level were calculated for each population pair. This hierarchical approach was applied over all loci for allozymes and microsatellites as well as for individual loci because in some instances statistically significant spatial variation was evident for a single locus but not for the marker class. The computer programs FSTAT, version 2.8 (Goudet, 2000), RST Calc, version 2.2 (Goodman, 1997), and ARLEQUIN, version 1.1 (Schneider et al., 2000) were used to compute $\hat{\theta}$, $\hat{R}_{ST}$, and $\hat{\Phi}_{ST}$.

The statistical significance of spatial and temporal variation in genetic diversity of walleye pollock was estimated by using F_{ST} estimator tests and allelic (haplotypic) goodness-of-fit tests (Goudet et al., 1996). First, the statistical significance of estimates for each F_{ST} analog ($\hat{\theta}$, $\hat{R}_{ST}$, and $\hat{\Phi}_{ST}$) was determined by using a permutation test option in the respective computer programs. In each case the data set was permuted 1000 times (alleles or haplotypes among population samples). Second, allele and haplotype frequency homogeneity was tested for the same population comparisons by using a G-test (allozymes and microsatellites) and probability test (mtDNA). The threshold for statistical significance (α=0.05) for multiple comparisons was determined by using the sequential Bonferroni method (Rice, 1989).

Results

Single-locus statistics and a comparison of marker classes

The degree of polymorphism indicated by the number of alleles per locus, allele frequency, and total heterozygosity (H_T) varied across loci and marker classes and was generally lower for allozymes than for microsatellites (Table 3). The number of alleles per allozyme locus ranged from two to nine (mean=four) and the frequency of the common allele in the pooled population sample was greater than 0.950 for all but four loci (*ALAT**, *MPI**, *PGDH**, and *SOD-2**, Table 3). In contrast, the number of alleles per locus was higher for microsatellites (range=12–32, mean=20), and the maximum allele frequency did not exceed 0.400 (Table 3). Relatively high polymorphism was also detected from restriction digests of ND5/6, cytochrome *b*, and cytochrome oxidase I regions of mtDNA (66 composite haplotypes, maximum haplotype frequency 0.371, Table 3). Values of mean $\hat{H}_T$ were an order of magnitude greater for microsatellites (0.769) than for allozymes (0.069); however, some overlap in range was evident because of the large variation in $\hat{H}_T$ among loci (Table 3). The estimate of haplotype diversity ($\hat{h}$=0.837) was slightly greater than the $\hat{H}_T$ for microsatellites (Table 3).

Values for $\hat{\theta}$ and $\hat{\Phi}_{ST}$ varied among loci and failed to expose a single marker class, regardless of overall variability, as most informative for detecting population structure in walleye pollock (Table 3). Permutation tests revealed two allozyme loci (*MPI**, *SOD-2**) and one microsatellite (*Tch22*) with $\hat{\theta}$ values significantly greater than zero over all population samples (Table 3, Fig. 2). The $\hat{\theta}$ of 0.088, for *SOD-2** was exceptionally high. The $\hat{\Phi}_{ST}$ for mtDNA was within the range of $\hat{\theta}$ for allozymes and microsatellites and was significantly greater than zero (P<0.001).

Intrapopulation genetic variation and Hardy-Weinberg equilibrium

Estimators of intrapopulation diversity (alleles per locus, $\hat{H}_E$ and $\hat{h}$) differed among marker types within populations but generally showed little variation between populations (Table 4). As expected, the values for the diversity estimators were usually lowest in the population with the smallest sample sizes (e.g. UNI, n=40). This was most notable in haplotype number (range 12–27) because most

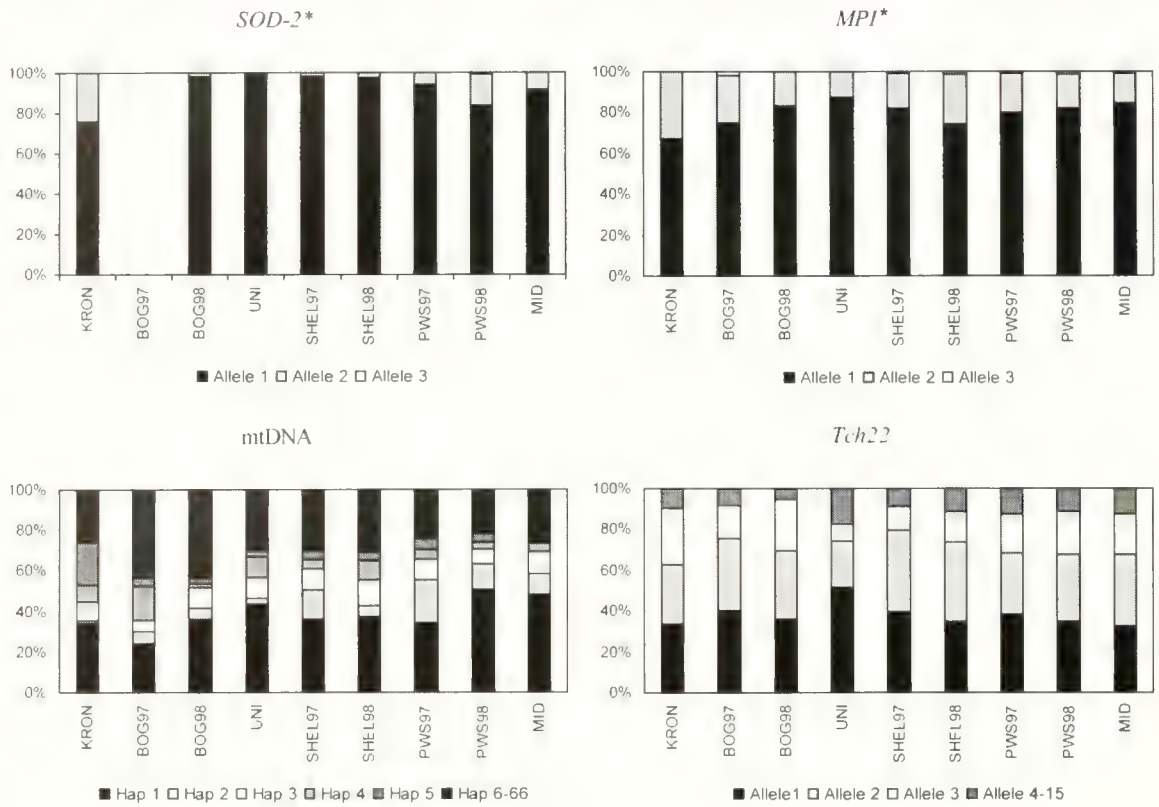

Figure 2

Frequency histograms for *SOD-2**, *MPI**, and *Tch22* alleles, and mtDNA haplotypes. Abbreviations: Kronotsky Bay (KRON); Bogoslof Island, 1997 (BOG97); Bogoslof Island, 1998 (BOG98); Unimak Pass (UNI); Shelikof Strait, 1997 (SHEL97); Shelikof Strait, 1998 (SHEL98); Prince William Sound, 1997 (PWS97); Prince William Sound, 1998 (PWS98); Middleton Island (MID). *SOD-2** data were not available for BOG97.

Table 4

Population statistics: mean number of individuals (n); mean number of alleles (A); expected heterozygosity ($\dot{H}_E$); analog of Wright's F_{IS} (f); haplotype diversity (h). Values in bold type with an asterisk are statistically significant. The α-level (0.05) was adjusted (α/k) for k tests, where k is the number of populations (9). SHEL = Shelikof Strait: PWS = Prince William Sound; MID = Middleton Island; BOG = Bogoslof Island; UNI = Unimak Pass; and KRON = Kronotsky Bay.

		Allozyme				Microsatellite				mtDNA		
Population	Year	n	A	$\dot{H}_E$	$\dot{f}$	n	A	$\dot{H}_E$	$\dot{f}$	n	A	$\dot{h}$
North America–Gulf of Alaska												
SHEL	1997	79.7	2.0	0.061	–0.002	80.0	12.0	0.762	0.037	99	27	0.832
	1998	99.7	2.1	0.064	0.023	84.3	12.3	0.774	0.021	72	22	0.828
PWS	1997	99.4	2.2	0.065	0.012	75.0	14.7	0.757	0.002	99	20	0.820
	1998	99.8	2.2	0.069	0.020	95.3	14.0	0.778	0.066	65	16	0.718
MID	1998	99.6	2.3	0.064	0.033	91.7	13.7	0.735	0.018	75	19	0.743
North America–Bering Sea												
BOG	1997	99.5	2.3	0.079	0.015	44.3	11.0	0.777	0.100	99	25	0.885
	1998	99.1	2.2	0.068	0.073	91.7	13.3	0.773	**0.094***	75	21	0.838
UNI	1998	39.8	1.5	0.062	0.007	40.0	10.3	0.746	**0.159***	30	12	0.786
Asia–eastern Kamchatka												
KRON	1999	92.0	2.0	0.080	–0.011	81.7	14.0	0.766	0.008	70	19	0.822
Mean		89.8	2.1	0.068	0.020	76.0	12.8	0.763	0.048	76.0	20.1	0.808

of the rare haplotypes were found in large samples. For example, 52 of 66 composite haplotypes had frequencies of 1% or less and only three of these haplotypes were present in the UNI sample, but 8, 14, and 15 rare haplotypes were present in the three largest samples (PWS 1997, BOG 1997, SHEL 1997; Table 4).

Population genotypic frequencies generally did not deviate from Hardy-Weinberg expectations. Permutation tests for the statistic f, conducted independently for allozymes and microsatellites, were concordant for all but two populations (BOG 1998; UNI 1998). The observed value of f for microsatellites in these two populations was significantly greater than zero ($P<0.005$) when $\alpha=0.05$ was adjusted for nine simultaneous tests (Table 4).

Spatial structure in genetic variation

1997 Gulf of Alaska and Bering Sea Population structure among the three North America samples was evident from mtDNA (overall $\hat{\Phi}_{ST}=0.017$, $P=0.002$; Table 5). The hierarchical analysis indicated that the two Gulf of Alaska populations were genetically different from the Bering Sea population ($\hat{\Phi}_{ST}=0.028$, $P<0.001$) but were not distinguishable from each other (Table 5). These results were confirmed by goodness-of-fit tests of haplotype homogeneity. Spatial genetic structure among the 1997 samples was not evident from values of $\hat{\theta}$ over all allozymes and microsatellites (Table 5).

1998 Gulf of Alaska and Bering Sea, and 1999 eastern Kamchatka Indices of population structure for allozymes ($\hat{\theta}=0.017$, $P<0.001$) and mtDNA ($\hat{\Phi}_{ST}=0.021$, $P<0.001$) were similar over all population samples and larger than for microsatellites ($\hat{\theta}=0.002$, $P>0.050$; $\hat{R}_{ST}=0.001$, $P>0.050$; Table 5). Because the values of $\hat{\theta}$ and $\hat{R}_{ST}$ over all microsatellites and pop-ulations were not significant, analyses of population structure were conducted with only the allozyme and mtDNA data. Significant genetic differences were revealed between pooled samples from North America and Asia with allozymes ($\hat{\theta}=0.030$, $P<0.001$) and mtDNA ($\hat{\Phi}_{ST}=0.035$, $P<0.001$; Table 5), between samples from the Gulf of Alaska and Bering Sea with allozymes ($\hat{\theta}=0.005$, $P=0.006$), and within the Gulf of Alaska with allozymes ($\hat{\theta}=0.009$, $P<0.001$) and mtDNA ($\hat{\Phi}_{ST}=0.018$, $P=0.009$).

Values for $\hat{\theta}$ were considerably larger for *SOD-2** than for the two other informative markers *MPI**, and mtDNA (Table 6, Fig. 2). Estimates of F_{ST} from mtDNA and *MPI** for each of the regional comparisons were similar but the most informative microsatellite locus, *Tch22*, did not vary significantly among regions.

Based on permutation test results from the hierarchical analyses, estimates of genetic differentiation were computed for all population pairs by using both allozyme and mtDNA data, except for Gulf of Alaska versus Bering Sea populations (allozyme data only). Values of $\hat{\theta}$ (allozymes) and $\hat{\Phi}_{ST}$ for most pairwise comparisons from North America and Asia were relatively large and highly significant (Table 5). In contrast, values of $\hat{\theta}$ (allozymes) for most population pairs from the Gulf of Alaska and Bering Sea were relatively small, and only the UNI × SHEL and UNI × PWS pairs were significant ($\hat{\theta}=0.021$, $P<0.003$; $\hat{\theta}=0.017$, $P<0.006$). Pairwise comparisons within the Gulf of Alaska were significant for SHEL × PWS (allozymes, $\hat{\theta}=0.017$, $P<0.002$) and for SHEL × MID (mtDNA, $\hat{\Phi}_{ST}=0.025$, $P<0.007$; Table 5).

In goodness-of-fit tests, allele and haplotype frequency homogeneity were concordant with the statistically significant values of $\hat{\theta}$ (allozymes) and $\hat{\Phi}_{ST}$ for all populations and pooled samples within and between regions (Table 5). However, results from the two types of tests conflicted for some population pairs. For example, G-tests of allozyme data revealed significant genetic variation for two population pairs (BOG × PWS; BOG × MID; Table 5) for which $\hat{\theta}$ was not significant. In contrast, $\hat{\theta}$ was significant for two population pairs, KRON × PWS and UNI × SHEL, which were not genetically different based on G-test results. One population pair, PWS × MID, was genetically different in the probability test of mtDNA data, but $\hat{\Phi}_{ST}$ for this pair was not significant (Table 5).

Temporal change in genetic variation: Bogoslof Island, Shelikof Strait, and Prince William Sound

Significant temporal change in mtDNA variation was detected in one population, BOG, by using the probability test of haplotype homogeneity ($P<0.001$) and $\hat{\Phi}_{ST}$ ($P=0.003$, Table 5). The $\hat{\Phi}_{ST}$ was within the range of values described for spatial variation and indicated a significant interannual change in haplotype frequency. Interestingly, this interannual shift in genetic variation was not evident from allozymes and microsatellites. However, the single most-informative locus *SOD-2** was not analyzed in the BOG 1997 sample because heart tissue was not available. Also, variation at the locus *MPI**, although not statistically significant, suggested that the BOG replicates were genetically different ($\hat{\theta}=0.011$, $P=0.066$; Table 6). A similar indication of temporal genetic variation was detected in the PWS population for all allozymes ($\hat{\theta}=0.005$, $P=0.046$), but $\hat{\theta}$ was not significant when α was adjusted for three simultaneous tests (initial $\alpha=0.016$, Table 5). In this case *SOD-2** was resolved and exhibited significant genetic variation ($\hat{\theta}=0.047$, $P=0.004$; Table 6). The mtDNA data, although not significant, also provided an indication of temporal variation in the PWS population ($\hat{\Phi}_{ST}=0.012$, $P=0.055$; Table 6).

Discussion

Comparison of marker classes

Our empirical results support two tentative conclusions regarding the usefulness of these marker classes for detecting population structure in walleye pollock. First, high overall heterozygosity such as that observed in some microsatellites may not be a reliable indicator of power for detecting population differences in walleye pollock, regardless of spatial scale. This conclusion contrasts with some simulation studies that have shown a positive relationship between locus polymorphism and the power to

Table 5

Tests for spatial and interannual genetic variation in walleye pollock. Abbreviations are as follows: number of populations (N); Gulf of Alaska (GOA); Bering Sea (BS); North America (NA); Bogoslof Island (BOG); Shelikof Strait (SHEL); Prince William Sound (PWS); Kronotsky Bay (KRON); Unimak Pass (UNI); Middleton Island (MID). Values in bold type with an asterisk are statistically significant. The α-level (0.05) for pairwise comparisons was adjusted (α/k) for k tests, where k is the number of population pairs per grouping strategy. Allo = allozyme; msat = microsatellite. Pr - P = the P-value for the probability test.

		F_{ST} analog tests				Goodness-of-fit tests		
						G-test P		Pr - P
Grouping strategy	N	θ allo	θ msat	$\hat{R}_{ST}$ msat	$\hat{\Phi}_{ST}$ mtDNA	allo	msat	mtDNA
1997 populations	3	0.000	0.000	–0.005	**0.017***	0.711	0.585	**<0.001**
Between GOA and BS	3				**0.028***			**<0.001**
BOG × SHEL					**0.024***			**<0.001**
BOG × PWS					**0.029***			**<0.001**
Within GOA	2							
SHEL × PWS					–0.004			0.876
1998 populations, Asia	6	**0.017***	0.002	0.001	**0.021***	**<0.001**	0.106	**<0.001**
Between NA and Asia	6	**0.030***			**0.035***	**<0.001**		**<0.001**
KRON × BOG		**0.039***			**0.035***	**<0.001**		**<0.001**
KRON × UNI		**0.057***			0.024	**<0.001**		0.028
KRON × SHEL		**0.028***			**0.026***	**<0.001**		**<0.001**
KRON × PWS		**0.014***			**0.051***	0.016		**<0.001**
KRON × MID		**0.029***			**0.048***	**<0.001**		**<0.001**
Between GOA and BS	5	**0.005***			0.004	**<0.001**		0.070
BOG × SHEL		0.004				0.216		
BOG × PWS		0.010				**<0.001**		
BOG × MID		0.001				**0.007**		
UNI × SHEL		**0.021***				0.017		
UNI × PWS		**0.017***				**<0.001**		
UNI × MID		0.011				0.011		
Within BS	2							
BOG × UNI		0.000			–0.008	0.454		0.754
Within GOA	3	**0.009***			**0.018***	**0.040**		**<0.001**
SHEL × PWS		**0.017***			0.007	**0.006**		0.504
SHEL × MID		0.006			**0.025***	0.109		**<0.001**
PWS × MID		0.002			0.019	0.722		**<0.001**
Interannual (1997–98)								
Bogoslof Island	2	0.001	–0.002	–0.007	**0.023***	0.162	0.479	**<0.001**
Prince William Sound	2	0.005	0.002	0.003	0.012	0.212	0.363	0.641
Shelikof Strait	2	0.001	0.001	0.000	–0.003	0.618	0.030	0.804

resolve population differentiation (e.g. Rousset and Raymond, 1995; Goudet et al., 1996). Nevertheless, empirical support for this relationship is mixed (e.g. Pogson et al., 1995; Estoup et al., 1998; Scribner et al., 1998). We believe our results suggest that mutation, which varies among these marker classes, has relatively little bearing on detecting genetic variation among walleye pollock populations. Instead, spatial differentiation may be limited because populations are large (i.e. genetic drift is weak) and gene flow among populations is high. The fact that only one private allele was found at the most variable microsatellite locus (Middleton Island, locus *Tch10*, allele 147) is an argument for high gene flow. Further, the index of population structure $\hat{R}_{ST}$ (Slatkin, 1995) developed to reflect the high mutation rate and mutation process of microsatellites is no larger than $\hat{\theta}$. The similarity of these values suggests that gene flow is relatively high and that mutation has relatively little influence on population differentiation (Slatkin, 1995).

Our second conclusion is that balancing selection may influence some but certainly not all allozymes in walleye pollock, as posited for marine species exhibiting low variation in allozyme allele frequencies (Pogson et al., 1995). Our conclusion is supported by two observations. First, microsatellites and mtDNA provide no greater resolution of overall population structure than allozymes (Tables 5

Table 6

F_{ST} estimates for *SOD-2**, *MPI**, and mtDNA. Abbreviations are as follows: number of populations (*N*); Gulf of Alaska (GOA); Bering Sea (BS); North America (NA). Values in bold type with an asterisk are statistically significant.

		F_{ST} analog tests		
Grouping strategy	*N*	θ *SOD-2**	θ *MPI**	Φ_{ST} mtDNA
1997 populations	3	N/A	0.001	**0.017***
1998 populations, Asia	6	**0.095***	**0.028***	**0.021***
Between NA and Asia	6	**0.155***	**0.059***	**0.035***
Between GOA and BS	5	**0.043***	0.002	0.004
Within BS	2	0.001	0.000	0.000
Within GOA	3	**0.051***	**0.013***	**0.018***
Interannual (1997–98)				
Bogoslof Island	2	N/A	0.011	**0.023***
Prince William Sound	2	**0.047***	0.000	0.012
Shelikof Strait	2	0.000	0.011	–0.003

and 6). Second, two allozyme loci (*SOD-2**; *MPI**) provided the strongest evidence of regional genetic variation among the 1998 samples (Table 6). In fact, the locus *SOD-2** had exceptionally high values of θ for most regional comparisons in contrast to the other nuclear loci and mtDNA. Diversifying selection may be acting on this locus (e.g. Hudson et al., 1997); however, the general concordance between *SOD-2**, *MPI**, and mtDNA data suggests that the values of θ most likely reflect the influence of genetic drift (Table 6, Fig. 2).

Spatial structure in genetic variation

North America to Asia The signature of a major east–west division between Asian and North American walleye pollock was evident in our allozyme and mtDNA data but not in our microsatellite data. The results of our F_{ST} analog tests and goodness-of-fit tests confirm the findings of earlier studies (e.g. Iwata, 1975a, 1975b; Grant and Utter, 1980; Shields and Gust, 1995, Bailey et al., 1999) and add some new insight regarding genetic heterogeneity in walleye pollock from different geographic regions. For example, we confirm the significant *SOD-2** variation observed in the past but we also reveal that a second allozyme locus, *MPI**, exhibits substantial spatial variation at this geographic scale (Table 6, Fig. 2). Nevertheless, only these two loci and the mtDNA reveal genetic variation between these two regional groups although some of the other 25 nuclear loci screened were equally or more polymorphic (e.g. *ALAT**, *PGDH**, *Tch10*, *Tch11*, and *Tch22*). These results suggest that, despite broad spatial separation, Asian and North American walleye pollock populations are remarkably genetically similar. This outcome supports the notion that the effective population size in walleye pollock is large, the rate of genetic drift is very low, and migration despite physical distance is a strong homogenizing force.

North America–Bering Sea and Gulf of Alaska The allozyme and mtDNA provided discordant results with respect to inter- and intraregional population structure within North American walleye pollock. The most noteworthy instance was the contradictory evidence of genetic variation between populations from the Bering Sea and the Gulf of Alaska. That is, significant genetic differentiation between populations from these two regions was evident from both the allozymes and mtDNA, but in different years (Table 5). We believe that the intraannual differences between marker classes is an artifact due primarily to the lack of *SOD-2** data for the Bogoslof Island sample in 1997. The values of θ and Φ_{ST} were similar in magnitude for the 1998 Bering Sea and Gulf of Alaska comparison, but only θ was statistically significant (Table 5). This result appears to be due to the influence of *SOD-2** for which θ was 0.043 and highly significant ($P<0.002$, Table 6). The value of θ over all allozymes for the 1997 Bering Sea and Gulf of Alaska comparison might have been similar to or larger than the Φ_{ST} for mtDNA if the *SOD-2** data had been available for the 1997 Bogoslof Island sample.

The 1998 samples provided the first indication of statistically significant genetic variation among populations in the Gulf of Alaska with both allozymes and mtDNA. Populations from Prince William Sound and Middleton Island were genetically distinguishable from the Shelikof Strait population, but they were not distinguishable from each other. These results are important for two reasons. First, this is the first indication of limited gene flow between a fjord spawning population (Prince William Sound) in the Gulf of Alaska and the numerically dominant Shelikof Strait population which spawns over the ocean shelf. Obvious factors that may limit gene flow between these two populations are the differences in spawning habitat preference and the counterclockwise flow of the Gulf of Alaska gyre which prevents larval drift from Shelikof Strait to the Prince William Sound (Bailey et al., 1999).

Second, the Prince William Sound and Middleton Island populations may warrant consideration as a distinct stock, which should be managed independently of the Shelikof Strait population.

The significant genetic differences between population pairs in the Gulf of Alaska are alternately supported by allozymes and mtDNA. That is, the Shelikof Strait and Prince William Sound populations differ significantly according to the allozyme data but not the mtDNA data, and the Shelikof Strait and Middleton Island populations differ significantly according to the mtDNA data but not the allozyme data (Table 5). We believe that the significant variation observed for each population pair is, in fact, real but is not supported by both marker types because these populations differ at only three loci (*SOD-2**, *MPI**, mtDNA). Thus, it is reasonable to expect differences between the populations at one locus (in this case, the marker class) and not the others based solely on the random effects of genetic drift.

Temporal change in genetic variation: Bogoslof Island, Prince William Sound

In addition to evidence of spatial structure within the Gulf of Alaska, we found evidence of interannual variation in genetic diversity among replicate samples from Bogoslof Island (mtDNA) and Prince William Sound (allozyme *SOD-2**). In each case the statistically significant variation was evident at only one marker, although in each case a second marker showed noticeable, but not statistically significant, variation between years (e.g. Bogoslof Island, *MPI**—$\hat{\theta}$=0.011, P=0.066; Prince William Sound, mtDNA—$\hat{\Phi}_{ST}$=0.012, P=0.055). We believe there are four likely sources for this apparent temporal shift.

First, walleye pollock may experience high variability in reproductive success among spawning adults as has been shown, for example, in oysters (Hedgecock, 1994). Walleye pollock have many life history traits such as semiplanktonic larvae, high fecundity, and external fertilization in a variable environment (Hedgecock, 1994), that may result in highly variable reproductive success and may contribute to temporal instability, particularly in small census populations such as that in Prince William Sound.

Second, walleye pollock may have varying degrees and types of philopatry. For example, juvenile walleye pollock may recruit to any one of a number of spawning aggregations and then exhibit repeat spawning behavior as an adult (adult philopatry). Adult philopatry has been used to explain the temporal instability observed in Atlantic herring (*Clupea harengus*, [McQuinn, 1997]) and could explain the apparent heterozygote deficit at microsatellites in the Bogoslof Island 1998 and Unimak Pass 1998. Alternatively, the degree of philopatry in walleye pollock may be extremely low despite the spatial and temporal predictability of spawning aggregations.

Third, a source-sink type metapopulation relationship may exist between some walleye pollock populations (e.g., Shelikof Strait and Prince William Sound; Unimak Pass and Bogoslof Island). Bailey et al., (1999) suggested that a metapopulation theory may explain existing data on population structure and dynamics of walleye pollock. The temporal genetic variation we observed in Prince William Sound and Bogoslof Island is consistent with this theory. Other circumstantial evidence supporting a source-sink relationship among some walleye pollock populations includes the discovery of walleye pollock in Prince William Sound (sink) concurrent with the increase in biomass of walleye pollock in the neighboring Shelikof Strait (source).

Finally, our supposed temporal replicates may actually represent samples from different spawning aggregates that spawn in the same location but at different times of the year. This finding suggests that fine-scale, intra-annual, genetic variation exists among walleye Pollock that spawn in the same area but perhaps days or weeks apart.

Summary

Our results show that the genetic variation, as measured by F_{ST}, among spatially distinct spawning aggregations of walleye pollock is generally low and is similar to the spatial genetic variation observed in other gadids such as Atlantic cod and European hake, *Merluccius merluccius* (e.g. Ruzzante et al., 1998; Lundy et al., 2000). In contrast, evidence of temporal genetic variation in gadid fishes is equivocal. Although some populations of European hake exhibit interannual variation in gene frequencies (Lundy et al., 2000), Ruzzante et al. (1997) found no evidence of temporal instability in Atlantic cod. For walleye pollock more detailed studies are needed to determine the extent to which all or some of the factors described above explain the temporal variability observed within some spawning aggregations. A priority of future genetic studies of walleye pollock should be to examine both fine-scale temporal variation (days and weeks within a year) and the genetic relationship among age cohorts from spatially distinct spawning aggregations. Because these studies will require extensive sampling, we recommend detailed examination of one or two spawning aggregations, such as those at Prince William Sound and Shelikof Strait. To further evaluate the metapopulation theory, candidate samples should include potential source populations (e.g. Shelikof Strait and Unimak Pass) and sink populations (e.g. Bogoslof Island and Prince William Sound). Future studies should also include a statistical examination of single locus $\hat{\theta}$ values to assess if *SOD-2** exceeds expectation and is perhaps influenced by a locus-specific force such as diversifying selection (e.g. Beaumont and Nichols, 1996).

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Abstract—Ninety-six bigeye tuna (88–134 cm fork length) were caught and released with implanted archival (electronic data storage) tags near fish-aggregating devices (FADs) in the equatorial eastern Pacific Ocean (EPO) during April 2000. Twenty-nine fish were recaptured, and the data from twenty-seven tags were successfully downloaded and processed. Time at liberty ranged from 8 to 446 days, and data for 23 fish at liberty for 30 days or more are presented. The accuracy in geolocation estimates, derived from the light level data, is about 2 degrees in latitude and 0.5 degrees in longitude in this region. The movement paths derived from the filtered geolocation estimates indicated that none of the fish traveled west of 110°W during the period between release and recapture. The null hypothesis that the movement path is random was rejected in 17 of the 22 statistical tests of the observed movement paths. The estimated mean velocity was 117 km/d. The fish exhibited occasional deep-diving behavior, and some dives exceeded 1000 m where temperatures were less than 3°C. Evaluations of timed depth records, resulted in the discrimination of three distinct behaviors: 54.3% of all days were classified as unassociated (with a floating object) type-1 behavior, 27.7% as unassociated type-2 behavior, and 18.7% as behavior associated with a floating object. The mean residence time at floating objects was 3.1 d. Data sets separated into day and night were used to evaluate diel differences in behavior and habitat selection. When the fish were exhibiting unassociated type-1 behavior (diel vertical migrations), they were mostly at depths of less than 50 m (within the mixed layer) throughout the night, and during the day between 200 and 300 m and 13° and 14°C. They shifted their average depths in conjunction with dawn and dusk events, presumably tracking the deep-scattering layer as a foraging strategy. There were also observed changes in the average nighttime depth distributions of the fish in relation to moon phase.

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Movements, behavior, and habitat selection of bigeye tuna (*Thunnus obesus*) in the eastern equatorial Pacific, ascertained through archival tags

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Bigeye tuna (*Thunnus obesus*) occur in subtropical and tropical oceanic waters throughout the world, except in the Mediterranean Sea (Collette and Nauen, 1983; Collette et al., 2001). They are captured by longliners operating in the eastern Pacific Ocean (EPO) from about 40°N to 40°S and by purse seiners from about 5°N to 10°S (Miyabe and Bayliff, 1998; Bayliff, 2000). They are economically the most important species of tuna harvested by longline fisheries in the EPO. The estimated average catch of bigeye tuna by the longline fleets of Japan, Taiwan, and the Republic of Korea in the EPO has declined from an average of about 79 thousand metric tons (t) during 1985–94 to about 40 thousand t during 1995–98 (Bayliff, 2000). The longline fishery targets medium to large bigeye tuna. There is a growing purse-seine fishery that catches primarily small to medium bigeye tuna, most of which are associated with drifting fish-aggregating devices (FADs). The purse-seine catch in the EPO has dramatically increased from an estimated annual average of about 5 thousand t during 1964–93, to about 45 thousand t during 1994–98 (Bayliff, 2000; Lennert-Cody and Hall, 2000). There is concern that the longline fishery is being adversely affected by the purse-seine fishery and that current catch rates are not sustainable (Watters and Maunder, 2001).

Elucidating the environmental variables that define bigeye tuna habitat can be used to adjust gear vulnerability, to standardize catch and effort data, and thus improve bigeye tuna stock assessments (Brill, 1994; Hinton and Nakano, 1996; Brill and Lutcavage, 2001; Hampton et al.[1]). It is also necessary to understand the affinity of bigeye tuna to drifting FADs, now a common feature of their habitat in the equatorial EPO, and to quantify the effect of FAD densities on vulnerability to capture. Sonic tracking studies (Holland et al., 1990; Holland et al., 1992; Daggorn et al., 2000), along with studies of catches per unit of effort (CPUEs) by longlines (Suzuki and Kume, 1982; Hanamoto, 1987; Boggs, 1992; Nakano et al., 1997) have provided information on differences in depth and temperature distributions for bigeye tuna by size and time of day.

Studies of fine-scale movements and short-term behavior, based on data from acoustic tags, have been reported for bigeye tuna associated with anchored FADs (Holland et al., 1990) and in the open ocean (Dagorn et al., 2000), but not for fish associated with drifting FADs. Bigeye tuna tend to stay within close proximity of anchored FADs during the day, move away at night, and return the next morning (Holland et al., 1990). When not associated with FADs, they swim within the mixed layer above the thermocline at night and well below the thermocline during

[1] Hampton, J., K. Bigelow, and M. Labelle. 1998b. Effect of longline fishing depth, water temperature and dissolved oxygen on bigeye tuna (*Thunnus obesus*) abundance indices. Working Paper 17, 18 p. Eleventh meeting of the standing committee on tuna and billfish, Sec. Pac. Comm., Noumea, New Caledonia. Oceanic Fisheries Programme, SPC, B.P. D5, 98848 Noumea Cedex, New Caledonia.

the day (Holland et al., 1990; Dagorn et al., 2000). They are capable of exploiting cold, deep waters below the thermocline because of their unique anatomy (Graham and Dickson, 2001), which enables them to physiologically and behaviorally thermoregulate by making vertical forays into the warm mixed layer throughout the day to increase their body temperatures (Holland et al., 1992, Holland and Sibert, 1994). Apparent differences in behavioral patterns of tunas around anchored FADs versus drifting FADs have been discussed, but almost no empirical results have been reported (Holland et al., 1990; Dagorn et al., 2000).

Although conventional and sonic tagging studies, and those on depth, temperature, and time of capture with longline gear, have provided valuable information on bigeye tuna biology and ecology, the present generation of archival (electronic data storage) tags can further our understanding of bigeye tuna movement, behavior, and habitat selection. Archival tags record swimming depth, internal and external temperatures, and ambient light levels. The light data can be processed to provide daily estimates of latitudes and longitudes (Hill, 1994; NMFS, 1994; Welch and Eveson, 1999; Hill and Braun, 2001).

This study presents results from analyses of data recorded by archival tags recovered from bigeye tuna that were released in the equatorial EPO during April 2000. An evaluation of the accuracy and precision of the geolocation estimates derived from the archival tag data is provided. Descriptions of movement and behavioral patterns, and also habitat characteristics of bigeye, are presented.

Materials and methods

Tag releases

Bigeye tuna were captured, tagged, and released at three FADs in the equatorial EPO between 0°52′ and 2°01′N and between 95°24′ and 97°06′W, during the period of 15–22 April 2000. Tagging was conducted on the chartered FV *Her Grace*, a 17.7-m, 99 gross-t, United States west-coast-style live-bait pole-and-line vessel. The FADs were taken out of the water before the vessel left the tagging area in order to minimize the probability of short-term recaptures, and to permit the fish to disperse.

The archival tags used in this study were model Mk7 manufactured by Wildlife Computers (Redmond, WA) (Wildlife Computers, 2002). The total weight of a tag in air is about 32 g. The Mk7 tag is designed for implantation into the peritoneal cavity of the fish so that the sensor stalk protrudes outside the fish through an incision in the abdominal wall. A label, printed in Spanish, with information about reporting the recovery of the tag and the associated reward (US$500) was encased in the epoxy of the main body of the instrument.

The depth, internal and ambient temperatures, and light level were stored in the memory of the tag every 4 minutes. At this sampling rate, the memory of each tag (2 MB) was capable of storing 3.8 years of data. The pressure sensors measured over a range of –40 to 1000 m with 0.5-m resolution. The temperature sensors measured over a range of –40° to 60°C with 0.05°C resolution. The light sensors had a logarithmic range from 3×10^{-10} W.cm^{-2} to 1×0^{-2} W.cm^{-2}. Bright sunshine is approximately 2×10^{-3} W.cm^{-2}. Light-level readings of about 200 and 50 are observed in bright sunshine and in complete darkness, respectively. Exploratory analyses of our data indicated that the light sensor is able to identify dawn and dusk events at 300 m.

Each tag was rigorously tested and evaluated at sea before deployment in bigeye tuna. Tags were programmed to collect data from all four sensors at one-second intervals, placed in a nylon mesh bag with a Sea-Bird SBE-39 temperature-depth probe, and sent down to approximately 300 m. After retrieval, the data were downloaded from each tag and their performance was evaluated in relation to the temperature-at-depth data collected by the Sea-Bird SBE-39.

Bigeye tuna specimens were captured by using handline gear during the day and night. Each fish was brailed with a heavy-gauge aluminum rigid-framed net of knotless webbing and landed on a wet foam pad covered with smooth vinyl. The eyes of the fish were immediately covered with a wet synthetic chamois, the hook was removed, and the condition of the fish was determined. If the fish was in excellent condition (i.e. no damage to the eyes or gills and no significant bleeding), the surgery required for implanting the archival tag was initiated. An incision about 2 cm long was made in the abdominal wall about 10 cm anterior of the anus and about 2 cm to the left of the centerline of the fish. Special care was taken to cut through the dermis only and partially through the muscle, but not into the peritoneal cavity. A gloved finger was inserted into the incision and forced through the muscle into the peritoneal cavity. The tag, sterilized by soaking it in Betadine solution, was inserted, pointed end first, through the incision into the peritoneal cavity. The tag was then manipulated to the caudal end of the incision, and two sutures were placed rostral of where the stalk protruded to close the incision by using a sterile needle and suture material (Ethicon (PDS II) size 0, cutting cp-1, 70 cm).

Fish were also tagged with two serially numbered 12.5-cm green plastic dart tags (Hallprint, Pty., Holden Hill, Australia) by using tubular stainless steel applicators. Tags were inserted into the dorsal musculature with the barbed heads passing between the pterygiophores below the base of the second dorsal fin, from both sides of the fish. Information for reporting the recovery of the fish and for receiving the reward (US$500) for the return of the fish was printed in Spanish on these tags. Lastly, five to ten mL of 100-mg/mL oxytetracycline hydrochloride solution were injected into the dorsal musculature with a disposable automatic vaccinator.

The 96 bigeye tuna released with archival tags were measured to the nearest centimeter with a caliper (mean=109.2 cm FL, 95% CI=1.9 cm, range=88–134 cm). The fish were then picked up by hand and released back into the sea by one or more individuals standing in a rack at the stern of the vessel. The total time most of the fish were out of the water was recorded to the nearest second (mean=2:17, 95% CI=0:06, range=1:27–4:19, n=86). All

Table 1

Release and recapture information for 28 bigeye tuna from which archival tags were recovered. The fish lengths are those measured at release. The locations are given in decimal degrees (dd).

Tag no.	Fish length (cm)	Release			Recapture			Days at liberty
		Location (dd)		Date	Location (dd)		Date	
99-787	115	0.87 N	97.10 W	15 Apr 00	1.72 N	83.08 W	22 Aug 00	128.7
99-792	126	0.87 N	97.10 W	15 Apr 00	1.35 N	95.82 W	15 Oct 00	182.7
99-793	114	0.87 N	97.10 W	15 Apr 00	2.25 N	97.25 W	21 Mar 01	339.7
99-801	112	1.47 N	96.97 W	17 Apr 00	1.47 N	90.72 W	06 Jul 00	79.8
99-803	113	2.02 N	95.40 W	22 Apr 00	2.20 N	102.72 W	26 Jul 00	94.1
99-804	104	1.47 N	96.97 W	17 Apr 00	4.80 N	105.42 W	23 Dec 00	249.6
99-810	120	2.02 N	95.40 W	22 Apr 00	1.65 S	93.17 W	18 Jun 00	56.0
99-812	116	2.02 N	95.40 W	22 Apr 00	0.55 N	109.00 W	29 Sep 00	159.1
99-814	120	2.02 N	95.40 W	22 Apr 00	1.42 N	88.93 W	13 Jul 01	446.1
99-816	122	2.02 N	95.40 W	22 Apr 00	1.78 N	97.60 W	30 May 00	37.1
99-817	106	1.47 N	96.97 W	17 Apr 00	1.12 S	95.87 W	18 Jun 00	61.7
99-826	119	1.47 N	96.97 W	17 Apr 00	0.50 N	101.52 W	14 Jan 01	271.8
99-835	109	2.02 N	95.40 W	22 Apr 00	1.20 N	99.68 W	18 Jun 00	56.1
99-839	109	1.47 N	96.97 W	17 Apr 00	2.33 S	95.75 W	12 Jun 00	55.8
99-847	102	1.47 N	96.97 W	17 Apr 00	1.77 N	97.23 W	29 May 00	41.7
99-853	103	2.02 N	95.40 W	22 Apr 00	1.20 N	99.68 W	18 Jun 00	56.1
99-860	104	1.47 N	96.97 W	17 Apr 00	2.18 S	97.87 W	10 Jun 00	53.7
99-861	110	1.47 N	96.97 W	17 Apr 00	2.23 S	96.67 W	04 May 00	16.8
99-862	93	1.72 N	96.80 W	18 Apr 00	1.77 S	94.80 W	21 Jun 00	63.7
99-864	110	2.02 N	95.40 W	22 Apr 00	2.70 N	97.87 W	17 May 00	24.1
99-865	101	1.47 N	96.97 W	17 Apr 00	2.67 S	99.05 W	15 Jun 00	58.6
99-869	113	1.08 N	97.08 W	16 Apr 00	4.85 N	103.18 W	07 Aug 00	112.4
99-874	108	1.47 N	96.97 W	17 Apr 00	2.70 N	97.87 W	17 May 00	29.8
99-877	88	1.08 N	97.08 W	16 Apr 00	2.77 S	99.20 W	08 May 00	21.4
99-883	116	1.93 N	96.55 W	19 Apr 00	1.60 S	95.55 W	18 Jun 00	59.7
99-884	102	0.87 N	97.10 W	15 Apr 00	1.12 N	86.18 W	01 Jul 01	441.7
99-889	112	1.08 N	97.08 W	16 Apr 00	0.37 N	98.58 W	02 Jul 00	76.4
99-891	124	2.02 N	95.40 W	22 Apr 00	0.25 S	92.88 W	01 May 00	8.1

fish released with archival tags were observed to swim rapidly down and away from the vessel after release, and all appeared to be in excellent condition.

Tag recoveries

Twenty-nine of the 96 bigeye released with archival tags were recaptured by 4 October 2001. Twenty-eight archival tags were recovered, and the data from twenty-seven were successfully downloaded and processed. The fish lengths, release and recapture positions, and number of days at liberty of the twenty-eight fish from which archival tags were recovered are given in Table 1. Twenty-five of the tags were recovered from fish caught by purse-seine vessels during sets on FADs. Scientific observers were aboard these purse-seine vessels, thus providing verification of recapture information. Three fish, from which archival tags (99-793, 99-812, and 99-865) were recovered, were recaptured by longline vessels without scientific observers aboard.

Data processing

Data were downloaded, decoded, and processed by using software provided by the tag manufacturer (Wildlife Computers, 2002). Light-level data were used to obtain daily position estimates for each fish and ranges of uncertainty about those estimates (Hill, 1994; Hill and Braun, 2001). The accuracy and precision of the position estimates were evaluated by calculating the differences between the known recapture locations for 21 bigeye tuna, determined by global-positioning systems (GPS) aboard the fishing vessels, and the corresponding geolocation estimates.

Two criteria were used for filtering (accepting or rejecting) daily geolocation estimates. The first was based on the uncertainty associated with estimates of latitude for the days of recapture, and the second was based on the distance between geolocation estimates for consecutive days. Those daily estimates in which the range between the north and south errors was greater than 6° or the location was farther than 4° in latitude from that for the

previous day were considered improbable and excluded from further analyses. For the 22 bigeye tuna at liberty for at least 30 days, this filtering procedure retained an average of 48.8% (95%CI=7.8%, range=15.3% to 76.5%) of the daily geolocation estimates. This procedure provided data sets of geolocation estimates throughout the period of time at liberty for each fish, about which we have a high level of confidence based on the expected accuracy and precision of these data (accuracy being the closeness of geolocation estimates to the actual position and precision the closeness or dispersion of repeated estimates [Kendall and Buckland, 1982]).

Each set of filtered geolocation estimates for individual bigeye tuna was integrated into a Geographic Information System (GIS). The animal movement analyst extension (AMAE) (Hooge and Eichenlaub, 1997; Hooge, et al.[2]) and the ArcView (Environmental Systems Research Institute, Inc., Redlands, CA) GIS program were used for mapping movement paths and for performing various spatial analyses of the data. The site-fidelity test in AMAE, employing 1000 random walks, was used to test the null hypothesis of random movement. The test is a modified Monte Carlo random walk, starting at the location of release, constrained by the coastline, and uses the actual sequence of distances between geolocation estimates to determine walk points. The fixed kernel home range model in the AMAE, which incorporates a least-squares cross-validation smoothing function, was used to assess probabilistic home ranges of fish for which the null hypothesis was rejected in the site-fidelity test. The 95% and 50% utilization distributions (probability contours) were chosen to describe the areas probably used (95%) and the probable core areas (50%) of activity, respectively, of individual fish.

For fish at liberty for 30 d or more, the behavior for each day at liberty was classified as unassociated (with a floating object) type-1, unassociated type-2, or associated with a floating object. Type-1 behavior is defined as that in which the fish primarily occupies the mixed layer during the night, descends at dawn below the thermocline to depths greater than 100 m and remains below 100 m throughout the day (aside from vertical forays into the mixed layer with a frequency of no more than 12 per day) and then ascends back into the mixed layer at dusk. This basic pattern has been described by Holland et al. (1990) and Dagorn et al. (2000), based on sonic tracking studies of bigeye tuna. Data from periods immediately after release at FADs until the time the FADs were removed and the data immediately preceding recapture at FADs were evaluated to determine criteria for classifying behavior of fish associated with floating objects. The percentages of time that 19 bigeye tuna spent at depths greater than 50 m, within 24-h intervals, for a total of 74 days, ranged from 0.0% to 29.1%. Sixty-nine percent of the 24-h intervals indicated that 16% or less time was spent below 50 m. The days when the fish were below 50 m for 16% of the time or less were classified as behavior associated with a floating object, and the days in which that time was greater than 16% were classified as unassociated type-2 behavior. For each fish, the numbers and durations of each behavioral event were determined throughout the period at liberty. A statistical test for a difference between the spatial distributions of the geolocation estimates for unassociated and associated behavior was conducted (Syrjala, 1996).

Dives in excess of 500 m were classified as deep dives, and the time, duration, and maximum depth of each event was determined for each bigeye tuna throughout periods at liberty. For those dives in which the pressure sensor reached its limit, at approximately 1000 m, depth was estimated from the ambient temperature value recorded by the tags by using historical annual mean temperatures at depths for the area of the deep diving event (Levitus and Boyer, 1994). The light level and ambient temperature data recorded by tags from bigeye tuna making dives in excess of 500 m indicated that light was essentially nonexistent below 500 m and that the ambient temperature was less than 8.5°C.

The archival tag data sets (for each recaptured bigeye tuna at liberty for at least 30 d) were separated into periods of nighttime and daytime by using light-level records. Nighttime was classified as the period between the time of the first record after dusk when there was no recognizable light from the sun until the time of the last record (before dawn) of no recognizable light from the sun. The individual data sets for night and day were used in evaluations of diel differences in behavior and habitat selection. The data for each night were classified by the moon phase (U. S. Naval Observatory, 2001). The classification scale used was 1 through 29 for the entire moon phase cycle. We analyzed changes in average daytime and nighttime depths for 20 individual bigeye tuna in relation to the visible disk area of the moon.

Results

Behavior

Evaluation of the depth and temperature records for bigeye tuna carrying archival tags resulted in the discrimination of four distinct behaviors: 1) unassociated type-1, 2) unassociated type-2, 3) associated with a floating object, and 4) deep diving. For the 23 fish at liberty for 30 or more days, behavior was classified for each day at liberty, and the duration of each behavior was determined (Table 2).

The behaviors of fish released or recaptured at FADs were distinct and discernible from the behaviors after the FAD was removed until the fish associated with the FAD at which it was recaptured (Fig. 1). Fish released at FADs showed a consistent swimming depth, predominantly less than 50 m during the night and day. When the FAD was removed fish showed an erratic up-and-down swimming behavior, followed by a consistent pattern of shallow (less

[2] Hooge, P. N., W. Eichenlaub, and E. K. Solomon. 2001. Using GIS to analyze animal movements in the marine environment. *In* 2001, spatial processes and management of marine populations (G. H. Kruse, N. Bez, A. Booth, M. W. Dorn, S. Hills, R. N. Lipcius, D. Pelletier, C. Roy, S. J. Smith, and D. Witherell, eds.), 20 p. Univ. Alaska Sea Grant, P.O. Box 755040, Fairbanks, AK 99775-5040.

Table 2

Summary statistics for the classification of daily behavior of 23 bigeye tuna at liberty for 30 days or more. The definitions for the four behavioral types and the classification criteria used are given in the text. The percentage of the total days at liberty for which an individual was classified as exhibiting a behavioral type is given as % days. The total number of events observed and classified in each dataset for a behavioral type and the mean duration for those events are given. Durations are given in days, except for deep diving events, which are given in hours.

	Unassociated type-1			Unassociated type-2			Associated			Deep diving	
Tag no.	% days	events	$\bar{x}$ duration	% days	events	$\bar{x}$ duration	% days	events	$\bar{x}$ duration	events	$\bar{x}$ duration
99-787	64.7	8	10.4	22.5	8	3.6	12.8	5	3.3	1	0.9
99-792	37.6	16	4.3	41.9	15	5.1	37.5	5	7.5	14	1.5
99-793	41.0	19	7.0	49.9	24	6.5	9.2	7	4.1	4	2.2
99-801	64.5	5	10.3	13.5	3	3.6	22.0	4	4.4	5	1.2
99-803	59.2	7	8.0	15.9	6	2.5	24.9	7	3.4	2	1.1
99-804	41.9	13	5.7	45.7	14	5.7	12.3	6	3.6	5	0.5
99-810	79.0	5	8.9	2.6	2	0.7	18.4	6	1.7	6	0.7
99-812	49.9	20	4.0	34.6	19	2.9	15.4	10	2.5	10	1.7
99-814	48.5	41	4.3	43.9	43	3.7	7.6	12	2.3	22	1.7
99-816	68.1	3	8.5	30.6	3	3.8	1.3	1	0.5	5	1.1
99-817	43.4	5	5.4	33.3	6	3.4	23.3	4	3.6	1	0.7
99-826	59.5	18	9.0	33.0	18	5.0	7.5	6	3.4	10	1.0
99-835	79.5	4	11.2	1.5	2	0.4	19.0	4	2.7	0	—
99-839	70.3	5	7.9	8.9	3	1.7	20.8	3	3.9	3	1.7
99-847	35.3	6	2.5	38.0	6	2.7	26.7	3	3.7	0	—
99-860	45.4	7	3.5	40.4	5	4.4	14.2	5	1.5	0	—
99-862	50.2	5	6.4	10.8	5	1.4	39.0	7	3.6	3	0.6
99-865	52.0	5	6.1	22.3	8	1.6	25.7	5	3.0	7	1.0
99-869	42.2	8	6.0	38.6	6	7.3	19.2	5	4.3	0	—
99-874	36.0	2	5.4	35.5	4	2.7	28.5	4	2.1	1	0.3
99-883	69.6	7	6.0	14.4	7	1.2	16.0	5	1.9	5	1.0
99-884	41.4	25	5.3	40.0	31	4.1	18.6	23	2.6	10	1.0
99-889	69.6	6	8.9	20.4	7	2.2	10.0	3	2.6	3	2.3
Mean	54.3	10.4	6.7	27.7	10.7	3.3	18.7	6.1	3.1	5.1	1.2
95%CI	6.1	4.0	1.0	6.2	4.5	0.8	4.0	1.9	0.6	2.3	0.3

than about 50 m) depths at nighttime and depths of about 200 to 300 m during the daytime (during the latter period vertical forays were made toward the surface [Fig. 1A]). Fish at FADs prior to recapture consistently swam at less than 50 m during the day and night, but made excursions to depths of 200 to 300 m for about 2 hours in the late afternoon. It was almost always apparent when a fish associated with a FAD because there was a change in swimming depths and behavior, specifically during the daytime (Fig. 1B).

Unassociated type-1 behavior

Type-1 behavior of bigeye tuna in the equatorial EPO was exhibited by fish not associated with FADs or other floating objects. The fish remained at 10 to 50 m at night and at 200 to 350 m during the day but undertook brief vertical forays into the mixed layer throughout the day (Fig. 2). The percentage of total days classified as type-1 behavior for individual fish ranged from 35.3% to 79.5% (mean=54.3%, 95% CI=6.1%). The mean duration of type-1 behavior ranged from 2.5 to 11.2 d (grand mean=6.7 d, 95% CI=1.0 d) (Table 2). The distribution of the durations of the 240 type-1 behaviors is shown in Figure 3A.

The differences in behavior between a 93-cm (tag 99-862) and 116-cm (tag 99-883) bigeye tuna within one week after release at the same FAD, both exhibiting type-1 behavior, are illustrated in Figure 4. Both fish showed the characteristic diel shifts in depth distribution at dawn and dusk. However, the 116-cm fish showed a shallower and less variable swimming depth at night and undertook fewer vertical forays during the daytime than did the 93-cm fish (Fig. 4A). The difference in the number of vertical forays by these two fish is explained by the more rapid rate of heat loss by the smaller individual, as indicated by the differences between the peritoneal cavity temperatures and the ambient temperatures (Fig. 4B). The 116-cm fish was able to maintain its internal temperature for longer periods of time. Thus, although these two fish were at similar maximum depth during the day, the average depth during the day for the 93-cm fish was less because of the increased time spent undergoing vertical forays.

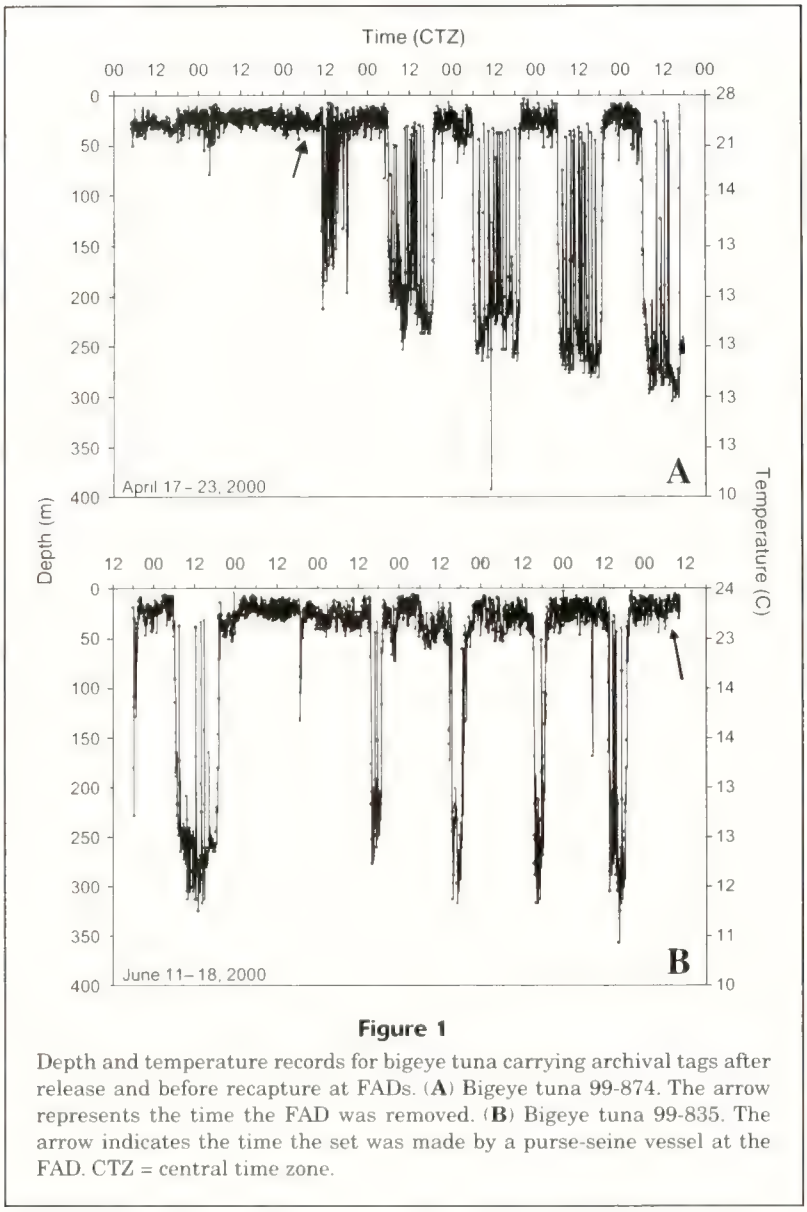

Figure 1

Depth and temperature records for bigeye tuna carrying archival tags after release and before recapture at FADs. (**A**) Bigeye tuna 99-874. The arrow represents the time the FAD was removed. (**B**) Bigeye tuna 99-835. The arrow indicates the time the set was made by a purse-seine vessel at the FAD. CTZ = central time zone.

Unassociated type-2 behavior

Type-2 behavior was defined as the behavior of fish that did not undergo the diel shifts in swimming depths at dawn and dusk but remained at depths in excess of 50 m for more than 16% of the time during a 24-h period (Fig. 5). The percentage of total days classified as type-2 behavior for individual fish ranged from 1.5% to 49.9% (mean=27.7%, 95% CI=6.2%). The mean duration of type-2 behavior for individual fish ranged from 0.4 to 7.3 d (grand mean=3.3 d, 95% CI=0.8 d) (Table 2). The distribution of the durations for each of the 245 type-2 behaviors is shown in Figure 3B.

Behavior associated with floating objects

Behavior associated with floating objects was defined as the behavior of fish that remained below 50 m for no more than 16% of the time throughout a 24-h period (Fig. 6). Although bigeye tuna mostly remained in the mixed layer while associated with floating objects, there was, nevertheless, a prominent diel cycle in the average depth distribution—from shallower at night to slightly deeper during the day (Fig. 6). The mean swimming depths for the data illustrated in Figure 6 are 27.7 m at night and 33.5 m during the day. The percentage of total days classified as associated behavior for individual fish ranged from 1.3% to 39.0% (mean=18.7%, 95% CI=4.0%). The mean duration of associated behaviors for individual fish ranged from 0.5 to 7.5 d (grand mean=3.1 d, 95% CI=0.6 d) (Table 2). The distribution of the durations of the 140 associated behaviors is shown in Figure 3C.

An examination of the classification of daily behavioral types by individual fish sorted by lengths (Table 2) indicated that a greater percentage of time was spent at FADs by bigeye tuna less than 110 cm in length (mean=23.3%,

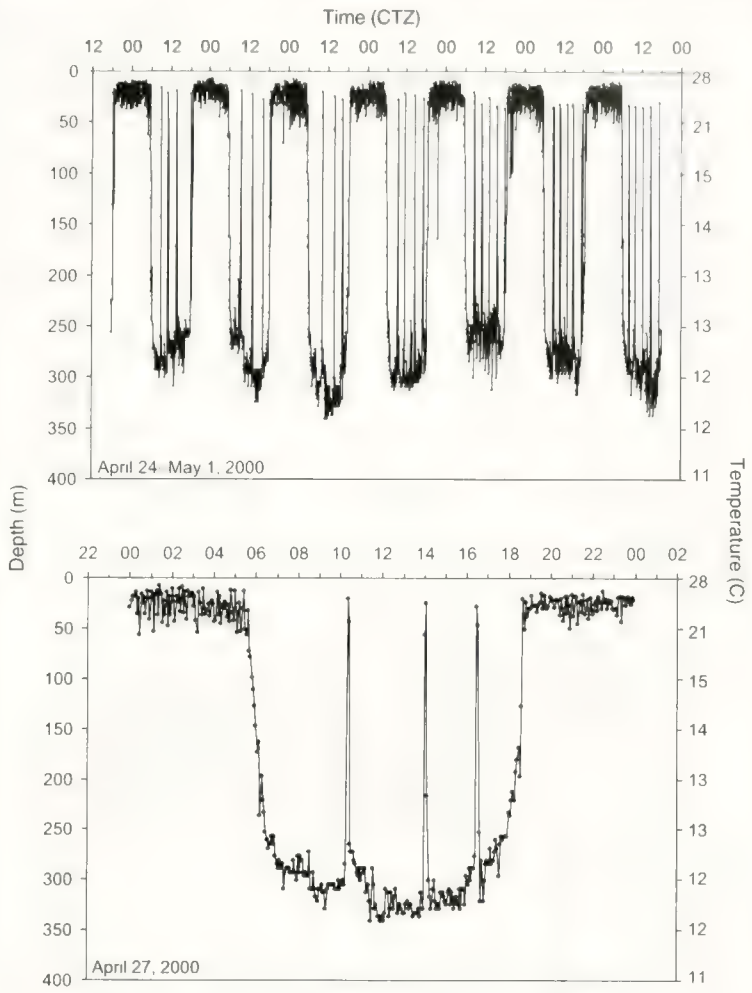

Figure 2

Depth and temperature records for a bigeye tuna carrying an archival tag (tag 99-889), exhibiting unassociated type-1 behavior. Approximate area, 1°N 97°W, is based on geolocation estimates from the archival tag. CTZ = central time zone.

n=9), even though the larger fish (mean=16.2%, n=12) still had an obvious affinity for floating objects.

Deep-diving behavior

Deep-diving behavior was defined as dives in excess of 500 m (Fig. 7). The mean duration of deep-diving behaviors for individual fish ranged from 0.3 to 2.3 h (grand mean=1.2 h, 95% CI=0.3 h) (Table 2). The distributions of the time of day, duration, and maximum depth of the 115 deep-diving events are shown in Figure 8. The majority of the deep dives occurred during daylight hours (mean=11:56 central time zone [CTZ]), although some deep dives were made at night. The prominent mode in the maximum depth distribution was about 650 to 850 m. The estimated maximum depth and minimum temperature reached by three bigeye tuna (99-801, 99-803, and 99-889) were 1500 m and 3°C, respectively.

Reliability of the geolocation estimates

The estimated mean accuracy and precision in the geolocation estimates of latitude were 2.04 and 0.79 degrees, respectively (Table 3). The associated uncertainty in those estimates averaged 2.57 degrees (95% CI=0.85) for the south error and 3.40 degrees (95% CI=1.00) for the north error. The estimated mean accuracy and precision of the geolocation estimates for longitude was 0.46 and 0.26 degrees, respectively (Table 3). The associated uncertainty in those estimates averaged 0.33 degrees (95% CI=0.13) for the west error and 0.17 degrees (95% CI=0.13) for the east error.

Additional information on the accuracy and precision of the estimates from the processed archival tag light-level data was obtained by comparing the differences between estimates and actual latitudes and longitudes of recapture for tags 99-864 and 99-874 (Table 3). The two bigeye tuna

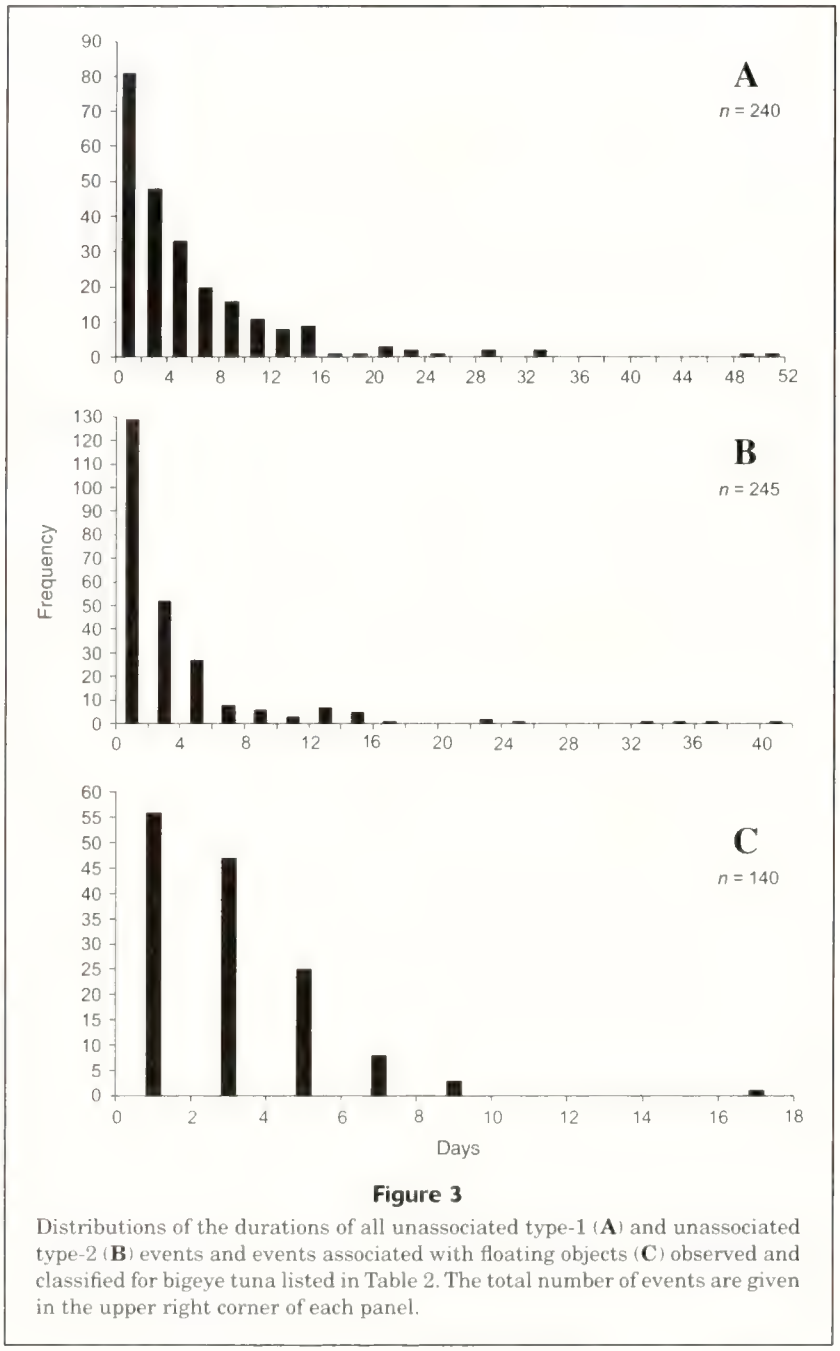

Figure 3

Distributions of the durations of all unassociated type-1 (**A**) and unassociated type-2 (**B**) events and events associated with floating objects (**C**) observed and classified for bigeye tuna listed in Table 2. The total number of events are given in the upper right corner of each panel.

carrying these tags were recaptured at the same location in the same purse-seine set. The respective differences between estimates and actual values were 0.20 and 0.30 for latitude and 0.23 and 0.06 for longitude. We also noted that the differences between estimated and actual latitudes and longitudes were 1.95 and 0.29, respectively, for the fish with tag 99-812, and 2.67 and 0.28, respectively, for the fish with tag 99-865 (Table 3). These two fish carrying these tags were recaptured by longline vessels, and scientific observers were not aboard to verify recapture positions.

Aside from the large differences between the estimates and actual recapture latitudes in Table 3 for tag numbers 99-801, 99-847, and 99-891, the majority of the estimates were within 2 degrees of the actual latitudes. Tags 99-792, 99-835, 99-861, and 99-877 were the only tags that provided differences more than 1 degree between the estimates and actual recapture longitudes.

Fish with tags 99-792, 99-793, 99-804, and 99-826 were at liberty during the autumn equinox. The geolocation estimates for longitude were unaffected by this event, but the estimates for latitude were unreliable for a few weeks

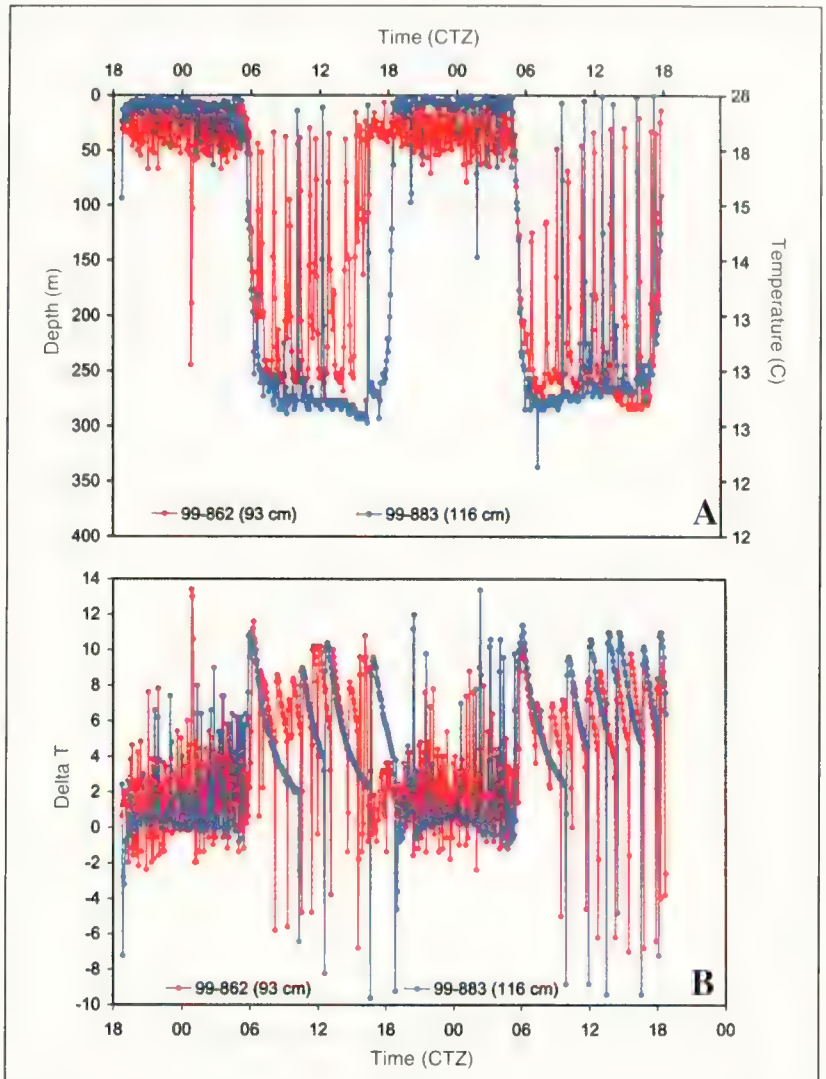

Figure 4

Simultaneous depth and temperature records for two bigeye tuna carrying archival tags, exhibiting unassociated type-1 behavior, 23–25 April 2000. Approximate area, 0°N 96°W, is based on geolocation estimates from the archival tags. (**A**) Depth and ambient temperature records (**B**) delta T's (differences between peritoneal cavity and ambient temperature) for the same time period as in A above. CTZ = central time zone.

surrounding the autumn equinox because there was very little variation in day length near the spring and autumn equinoxes (Hill and Braun, 2001).

Movements

The movements of 8 bigeye tuna at liberty for 76 to 340 days are plotted in Figure 9, A–D. No bigeye tuna went farther west than about 110°W and most spent the majority of time between 90°W to 105°W and 5°N to 5°S. Data for the estimated movement paths of 22 fish, derived from the filtered geolocation estimates, are given in Table 4. The estimated mean speeds ranged from 76 to 165 km/d (grand mean=116.6 km/d, 95% CI=10.0 km/d). The hypothesis that the observed movement path is random was rejected for 17 of the 22 fish (Table 4). A significant positive correlation (r=0.61, P<0.05) was found between the number of days at liberty and their corresponding 95% utilization distributions (Tables 1 and 4).

The areas encompassed by the 95% probability ellipses for the geolocation estimates of unassociated behavior and behavior associated with floating objects (Fig. 10), for the 22 bigeye tuna at liberty for 30 d or more (Table 4), were 3.9 and 3.1 × 10^6 km^2, respectively. The difference between

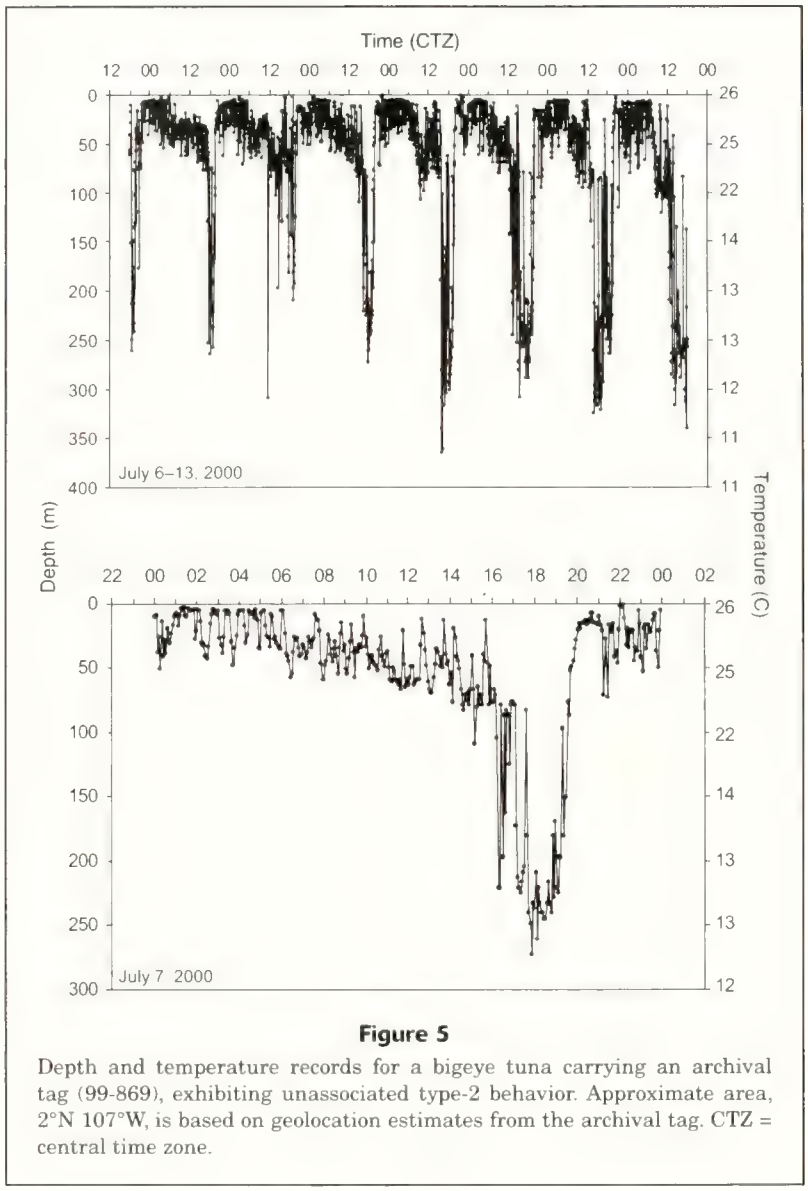

Figure 5

Depth and temperature records for a bigeye tuna carrying an archival tag (99-869), exhibiting unassociated type-2 behavior. Approximate area, 2°N 107°W, is based on geolocation estimates from the archival tag. CTZ = central time zone.

the two spatial distributions was not statistically significant (Ψ=0.313, P=0.524).

The fish with tag 99-793 was at liberty 340 d and exhibited behavior associated with floating objects for 9.2% of those days. It traveled initially to the east, remained for a considerable period in a relatively restricted area north of the Galapagos Islands, displayed some range in latitudinal movements between about 5°N and 5°S, and was recaptured only 83 nmi north of its release location (Fig. 9A, Tables 1, 2, and 4). The fish with tag 99-812 was released at a different FAD and was at liberty for a shorter period (159 d). It exhibited behavior associated with floating objects for 15.4% of the days at liberty. In contrast to the fish with tag 99-793, the fish with tag 99-812 traveled westward, displaying a fairly directed movement path, and was subsequently recaptured 821 nmi west of its release location (Fig. 9A, Tables 1, 2, and 4).

The fish with tag 99-826 was at liberty 272 d and exhibited behavior associated with floating objects for 7.5% of those days. It traveled the greatest total distance, displaying extensive longitudinal and latitudinal movements, and yet was recaptured only 279 nmi west of its release location (Fig. 9B, Tables 1, 2, and 4). The fish with tag 99-804 was released at the same FAD as the fish with tag 99-826 and was at liberty for a comparable period (250 d). It exhibited behavior associatede with floating objects for 12.4% of the days at liberty. In contrast to the fish with tag 99-826, the fish with tag 99-804 displayed a much more constrained movement path. This fish started moving to the northwest during its last few months at liberty and was subsequently recaptured 544 nmi west of its release location (Fig. 9B, Tables 1, 2, and 4).

The fish with tag 99-792 was at liberty for 183 d and exhibited behavior associated with floating objects for 37.5%

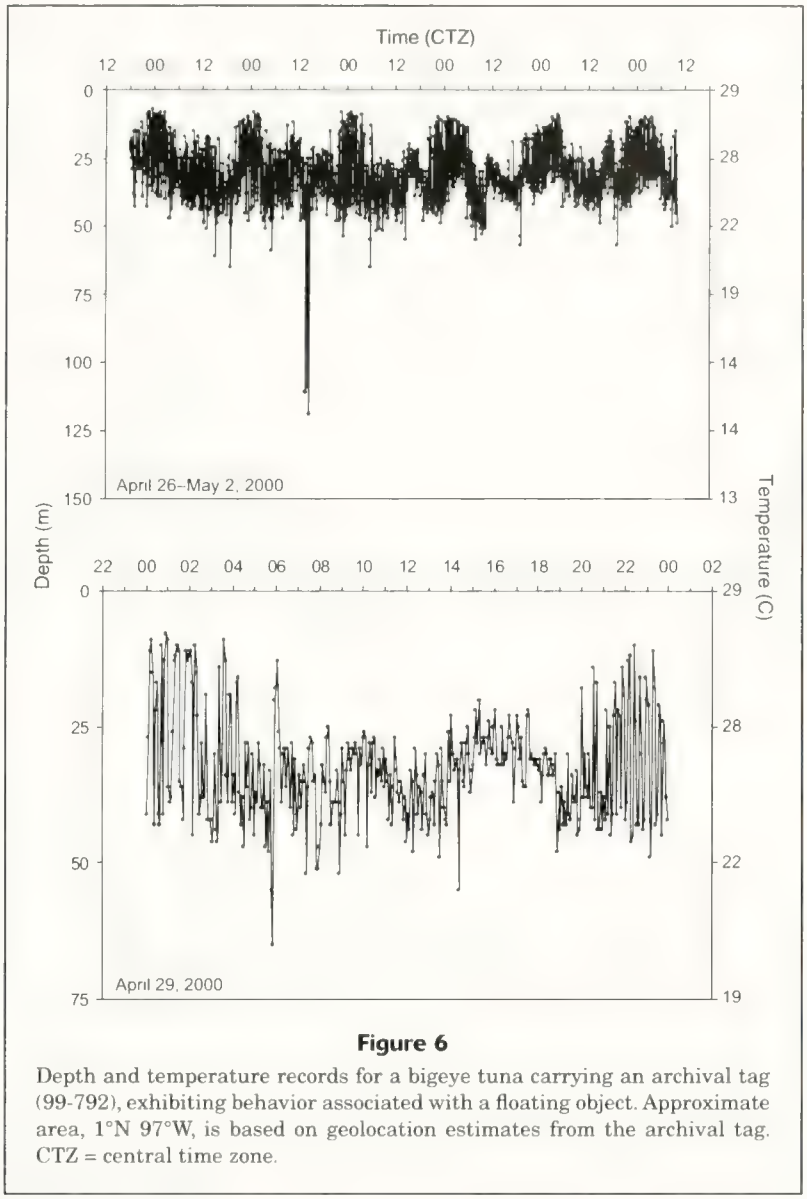

Figure 6

Depth and temperature records for a bigeye tuna carrying an archival tag (99-792), exhibiting behavior associated with a floating object. Approximate area, 1°N 97°W, is based on geolocation estimates from the archival tag. CTZ = central time zone.

of time at liberty. The fish traveled a considerable distance west and southwest to about 5°S and 110°W, before moving back toward the east. It was recaptured only 82 nmi east of its release location (Fig. 9C, Tables 1, 2, and 4). The fish with tag 99-787 was released at the same FAD where the fish with tag 99-792 was also released. It was at liberty for 129 d and exhibited behavior associated with floating objects for 12.8% of time at liberty. In contrast to the fish with tag 99-792, the fish with tag 99-787 traveled in the opposite direction, toward the east, moving fairly rapidly to around 82°W, and then moving north and south between about 3°N and 3°S. This fish was recaptured 843 nmi east of its release location (Fig. 9C, Tables 1, 2, and 4).

The fish with tag 99-889 was at liberty 76 d and exhibited behavior associated with floating objects for 10.0% of time at liberty. This fish traveled a considerable distance south to about 7°S, before moving back northward, and was subsequently recaptured only 100 nmi southwest of its release location (Fig. 9D, Tables 1, 2, and 4). The fish with tag 99-869 that was released at the same FAD where fish 99-889 was released, was at liberty 112 d and exhibited behavior associated with floating objects for 19.2% of time at liberty. The fish initially traveled in a similar direction as that of fish 99-889 before moving westward. It showed extensive latitudinal movements from about 5°S to 5°N, and was recaptured 430 nmi northwest of its release location (Fig. 9D, Tables 1, 2, and 4).

Habitat selection

The habitat selected by bigeye tuna is presented by month in Figure 11, for days with unassociated type-1 behavior only. The nighttime and daytime depth distributions were very similar for April, May, and June. Most of the time

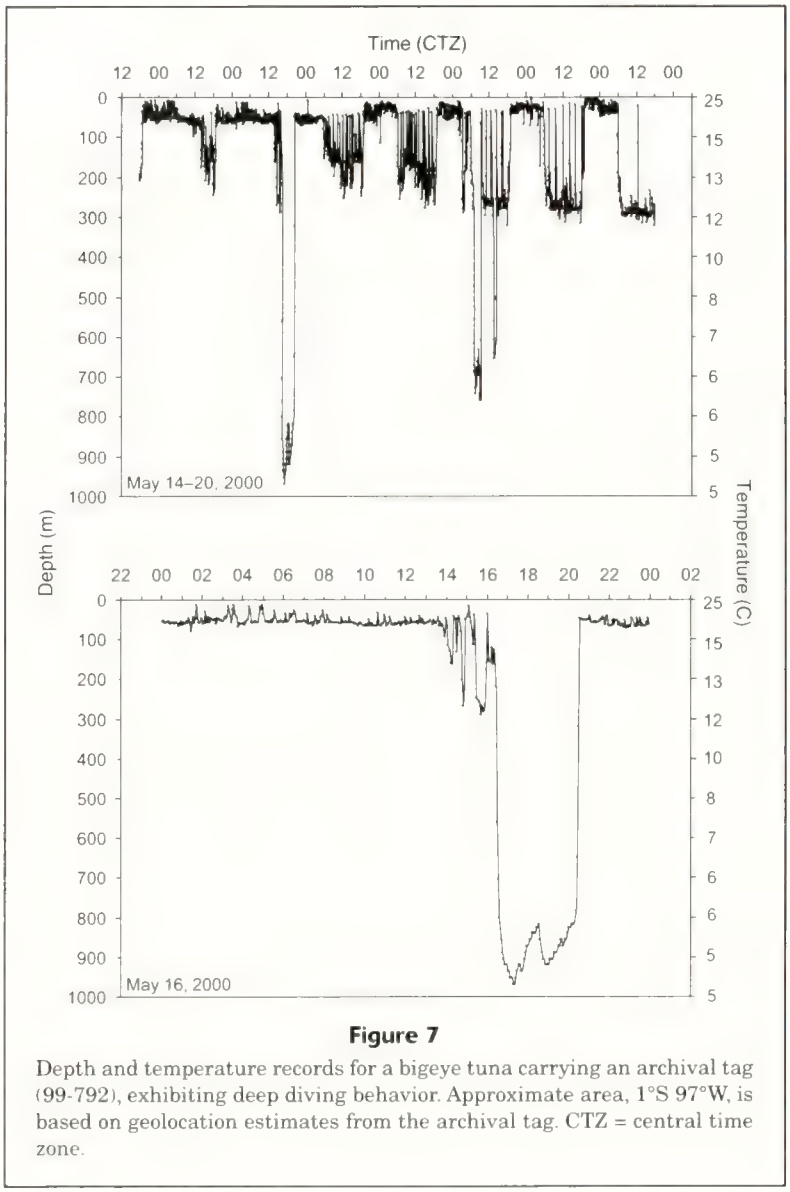

Figure 7

Depth and temperature records for a bigeye tuna carrying an archival tag (99-792), exhibiting deep diving behavior. Approximate area, 1°S 97°W, is based on geolocation estimates from the archival tag. CTZ = central time zone.

was spent above 50 m at night and between 250 to 300 m during the day. From April to June, the average depths of the 20°C and 15°C isotherms were 50 and 100 m, respectively. The habitat selected by the fish during July, August, and September was different and more variable during the day than that for the previous three months. Most of the time was spent above 50 m during the night. During the day the primary mode in depth in July was similar to the previous three months, but in August the primary mode shifted to about 200–275 m. In July the average depths of the 20°C and 15°C isotherms were 17 and 90 m, respectively, whereas in August and September the average depths of the 20°C and 15°C isotherms were 10 and 75 m, respectively. In September the depth distribution during the day was more uniform from about 100–350 m, with a slight mode between 175 and 250 m. The daily vertical behavior of the fish during September was highly unusual and erratic in relation to previous months and to October; 78% of the days for five fish were classified as unassociated type-2 behavior. The habitat selected by the fish during October, November, and December was different during the night, than that for the previous six months. Most of the time was spent above 25 m during the night. During the day the primary modes in depth during October, November, and December were not as distinct as in previous months, excluding September, but were primarily between 150 and 275 m. The average depths of the 20°C and 15°C isotherms for October and December were 15 and 75 m respectively, whereas in November the average depths of the 20°C and 15°C isotherms were 25 and 50 meters, respectively. The habitat selected by the fish during the day in January, February, and March was similar, with a distinct mode in depth between about 200 and 300 m. During the night, there was a transition

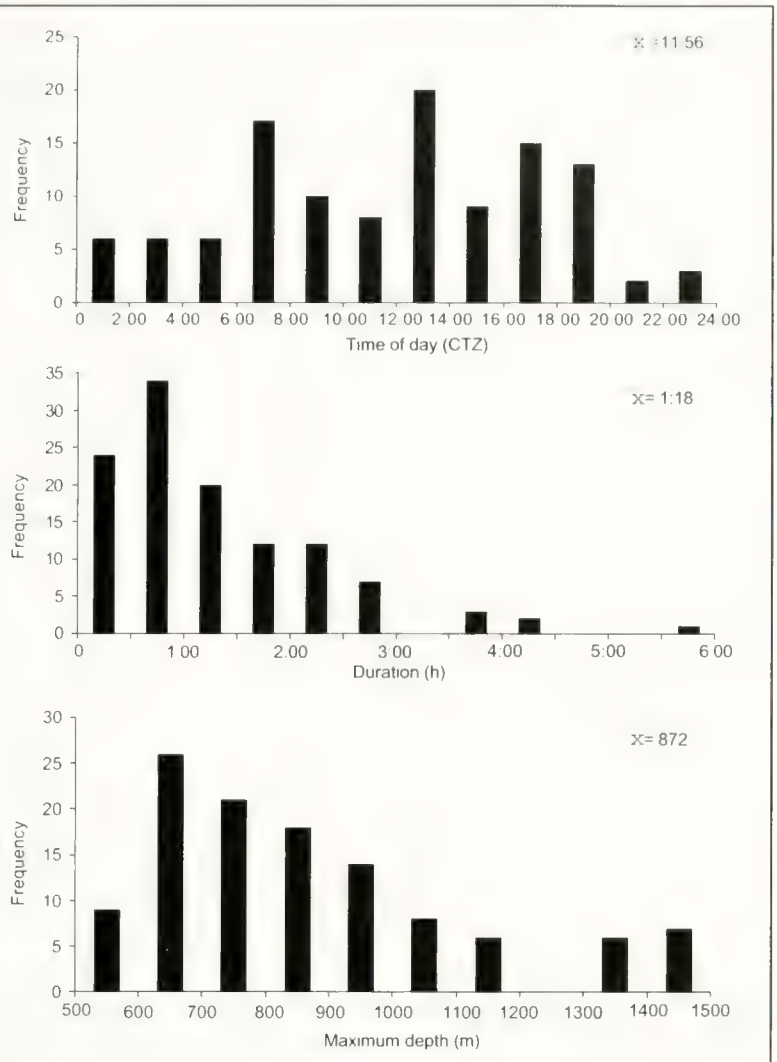

Figure 8

Distributions of the time of day, duration, and maximum depth for 115 deep-diving events observed and classified for bigeye tuna listed in Table 2. The average value is given in the upper right corner of each panel. CTZ = central time zone.

during these three months from most of the time being spent above 25 m in January to a greater amount of time spent between 25 to 50 m at night in March. This transition corresponded with a downward shift in the depths of the 20°C and 15°C isotherms from an average of 30 and 80 m in January and February to 50 and 100 m in March, respectively.

The percentages of time that 13 bigeye tuna (112–126 cm in length at release) spent within 25-m depth intervals from the surface to 400 m, during each hour of each day at liberty, while exhibiting unassociated type-1 behavior, are given in Table 5. The average daytime temperatures and depths for these fish throughout their times at liberty, when exhibiting type-1 behavior, indicated that the highest concentration (about 50%) were between 13° and 14°C and 200 and 300 m depth. About 85% of the data were distributed between 13° and 16°C and 150 and 300 m in depth.

Twelve of the twenty-two bigeye tuna showed significant correlations (r=0.61 to 0.75, P<0.05) between the visible disk area of the moon and their average nighttime depth distributions. There was a significant correlation (r=0.81, P<0.05) between the average nighttime depth for all 22 fish and the visible disk area of the moon (Fig. 12A). Fish occupied significantly greater depths for the 7-day period surrounding the full moon (29.0 m), in contrast to the other 22 days of the lunar cycle (21.2 m) (Fig. 12A). The average nighttime light levels indicated that the change in depth did not totally compensate for the greater light intensity during the full moon phase (Fig. 12A). Eight of the twenty-two fish showed significant correlations (r=0.54 to 0.75, P<0.05) between average daytime depth

Table 3

The accuracy, precision, and uncertainty in estimated latitudes and longitudes derived from archival tag light-level data from 21 bigeye tuna, processed with the geolocation programs of Wildlife Computers (Hill and Braun, 2001). The latitudes and longitudes are given as decimal degrees (dd). The error estimates are the uncertainty about the individual estimates of latitude or longitude. The differences are those between the actual latitude and longitude of recapture and the corresponding geolocation estimates.

	Recapture latitude (dd)					Recapture longitude (dd)				
Tag no.	Actual	Estimate	South error	North error	Difference	Actual	Estimate	West error	East error	Difference
99-787	1.72 N	1.0 N	2.5	2.5	0.72	83.08 W	82.97 W	0.5	0.0	0.11
99-792	1.35 N	3.0 N	3.0	4.0	1.65	95.82 W	93.93 W	0.5	0.0	1.89
99-801	1.47 N	5.0 S	1.5	4.5	6.47	90.72 W	90.62 W	0.5	0.0	0.10
99-803	2.20 N	1.0 N	2.5	2.0	1.20	102.72 W	102.12 W	0.5	0.0	0.60
99-810	1.65 S	2.5 S	1.5	2.0	0.85	93.17 W	93.21 W	0.0	0.5	0.04
99-812	0.55 N	2.5 N	0.0	2.0	1.95	109.00 W	109.29 W	0.0	0.5	0.29
99-816	1.78 N	1.5 N	3.0	3.5	0.28	97.60 W	97.40 W	0.0	0.5	0.20
99-817	1.12 S	2.0 S	3.5	5.5	0.88	95.87 W	95.47 W	1.0	0.0	0.40
99-835	1.20 N	5.0 N	2.5	2.5	3.80	99.68 W	98.48 W	0.5	0.0	1.20
99-839	2.33 S	0.0 N	6.5	0.5	2.33	95.75 W	95.54 W	0.5	0.0	0.21
99-847	1.77 N	3.0 S	2.5	5.0	4.77	97.23 W	97.17 W	0.0	0.5	0.06
99-860	2.18 S	2.0 S	3.0	2.0	0.18	97.87 W	97.20 W	0.5	0.0	0.67
99-861	2.23 S	1.5 N	6.0	6.5	3.73	96.67 W	95.56 W	0.0	0.0	1.11
99-864	2.70 N	2.5 N	1.0	3.0	0.20	97.87 W	98.10 W	0.5	0.5	0.23
99-865	2.67 S	0.0 N	1.5	6.5	2.67	99.05 W	99.33 W	0.5	0.0	0.28
99-869	4.85 N	4.0 N	2.5	2.0	0.85	103.18 W	103.35 W	0.5	0.0	0.17
99-874	2.70 N	3.0 N	1.0	2.0	0.30	97.87 W	97.81 W	0.5	0.0	0.06
99-877	2.77 S	2.0 S	7.0	3.0	0.77	99.20 W	97.37 W	0.0	1.0	1.83
99-883	1.60 S	0.5 N	0.5	0.5	2.10	95.55 W	95.67 W	0.0	0.0	0.12
99-889	0.37 N	2.5 S	1.5	2.5	2.87	98.58 W	98.57 W	0.0	0.0	0.01
99-891	0.25 S	4.5 S	1.0	9.5	4.25	92.88 W	92.74 W	0.5	0.0	0.14
Mean			2.57	3.40	2.04			0.33	0.17	0.46
95% CI			0.85	1.00	0.79			0.13	0.13	0.26

distributions and visible disk area of the moon. The patterns in average daytime depths for 5 of the 8 fish showed a significantly shallower depth distribution for a 3-day period surrounding the full moon (190 m) compared to the other 26 days of the lunar cycle (221 m). There was no apparent pattern, and the correlation coefficient (r=0.15, P>0.05) was not significant for the average daytime depth for all 22 bigeye tuna in relation to the visible disk area of the moon (Fig. 12B).

Discussion

The results obtained in our study are useful for evaluating fine- to large-scale horizontal and vertical movements, behavioral patterns, and habitat characteristics on spatial and temporal scales previously undocumented for bigeye tuna. Movement paths, residence times at FADs, and habitat selection are essential for understanding the ecology of this species, and should be incorporated into stock assessment models to evaluate its vulnerability to various modes of fishing.

In addition to the 96 bigeye tuna released with archival tags, we released 101 bigeye tuna, in the same area and time period, with conventional plastic dart tags only. To date, 29 (30%) of the fish with archival tags and 22 (23%) of these with conventional tags have been confirmed as recaptured. The difference between these percentages was not significant (P>0.05), indicating that tagging mortality was probably no greater for the fish with archival tags than the fish with conventional tags.

Several of the archival tags were removed from recaptured bigeye tuna by members of the scientific staff of the Inter-American Tropical Tuna Commission (IATTC). All but two of the tags were situated in the peritoneal cavity, in the general area where they were implanted, and were apparently encapsulated by fibrous connective tissue. Of the two other tags, one had apparently been invaginated into the lumen of the stomach and the other into the lumen of the intestine. Apparently the fish were attempting to expel these foreign bodies from their peritoneal cavities. Transintestinal expulsion of surgically implanted transmitters by fish was previously considered an exceptional phenomenon, except in the case of catfish (Marty and

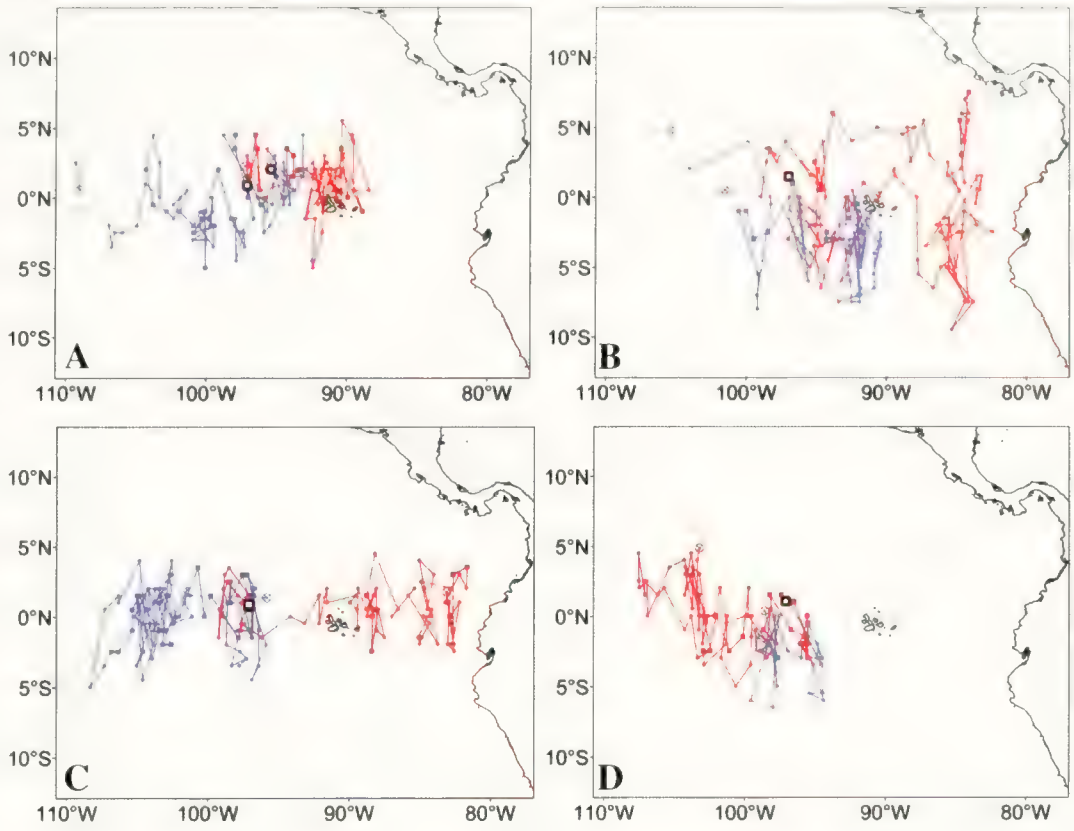

Figure 9

Movement paths of bigeye tuna derived from filtered geolocation estimates. The open squares are the release positions at FADs. The open circles and solid squares are geolocation estimates for unassociated behavior and behavior associated with a floating object, respectively, and the crosshairs are the recapture positions. The color code for each fish, in each map, corresponds with the following tag number. (**A**) blue: 99-812. The dashed line, between two geolocation estimates on 16 August and 27 September 2000, represents our inability to obtain reliable estimates of latitude from light level data near the equinox. red: 99-793. The dashed line, preceding the recapture position, represents our inability to obtain reliable estimates of latitude from light level data near the equinox and the failure of the tag to log data on 3 October 2000. (**B**) blue: 99-804. The dashed line, preceding the recapture position, represents the failure of the tag to log data on 9 October 2000. red: 99-826. The dashed line, between two geolocation estimates on 20 August and 4 October 2000, represents our inability to obtain reliable estimates of latitude from light level data near the equinox. The dashed line, preceding the recapture position, reflects the failure of the tag to log data on 25 December 2000 (**C**) blue: 99-792. The dashed line, beginning on 31 August 2000 preceding the recapture position, represents our inability to obtain reliable estimates of latitude from light level data near the equinox. red: 99-787. (**D**) blue: 99-889. red: 99-869.

Summerfelt, 1986; Baras and Westerloppe, 1999). In most specimens, the ventral region of the body wall, where the stalk protruded, did not appear to be completely healed. A small, dark, circular crater was seen at the base of the stalk—obviously a mark of irritation from the movement of the stalk even after the tag body had been encapsulated by flesh. Unless it is necessary to collect internal temperature data, the dorsal musculature is a potentially better location for implanting archival tags, of appropriate size and shape, for long-term deployment (Brill et al.[3]).

The long-term performance of the archival tags used in our experiment was questionable. The bigeye tuna that we studied pushed these tags to the limits of their design specifications by undergoing regular daily vertical forays with fairly dramatic temperature and pressure fluctuations, in addition to making the unexpected deep diving events exceeding 1000 m.

Of the 27 archival tags recovered to date, four of them failed to collect light data because of apparent problems

[3] Brill, R. W., K. Cousins, and P. Kleiber. 1997. Test of the feasibility and effects of long-term intramuscular implantation of archival tags in pelagic fishes using scale model tags and captive juvenile yellowfin tuna (*Thunnus albacares*). NMFS Admin. Rep. H-97-11,12 p. Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, HI 96822-2396.

Table 4

Spatial statistics for 22 bigeye tuna at liberty for 30 days or longer, based on filtered estimates of the geographic locations derived from the archival tag light level data. *n* is the total number of geographic locations in the data set. Distance is the total distance traveled per data set. Linearity is the ratio of the distance between the data set endpoints and the total distance traveled. MSD is the mean squared distance from the center of activity. *p* is the proportion of MSD values, from a Monte Carlo simulation, higher than the MSD value from the observed data. UD is the utilization distribution, for the 95% and 50% probability levels, reported as area in km^2. NA stands for non applicable because those estimates are only valid if the movement path indicates site fidelity.

Tag no.	*n*	Distance (km)	*x* bearing	$\bar{x}$ speed (km/d)	Linearity	MSD (km 10^9)	Site fidelity (*p*)	95% UD (km^2)	50% UD (km^2)
99-787	75	13596	11	105	0.12	408.017	59.6	NA	NA
99-792	94	20017	217	142	0.01	195.310	99.7	1,182,310	131,437
99-793	52	11996	30	86	0.06	111.726	99.9	793,555	103,429
99-801	32	7513	171	94	0.09	227.857	78.9	NA	NA
99-803	72	11721	186	123	0.08	134.198	95.3	802,037	100,354
99-804	75	17044	219	115	0.06	218.924	98.4	1,169,153	104,391
99-810	33	6975	51	122	0.05	79.566	99.9	430,586	83,410
99-812	78	14603	182	92	0.11	262.036	84.2	NA	NA
99-814	70	17671	138	143	0.02	109.497	99.9	836,649	158,936
99-816	27	4752	309	128	0.08	62.609	96.7	393,121	49,882
99-817	36	7970	158	129	0.03	83.159	99.9	478,858	50,205
99-826	108	23,085	219	113	0.03	494.010	78.9	NA	NA
99-835	37	6785	183	119	0.09	111.445	91.9	NA	NA
99-839	24	6143	267	110	0.03	90.090	99.4	501,057	107,094
99-847	11	3188	126	76	0.04	113.948	96.3	516,561	145,177
99-860	38	8893	324	165	0.02	65.013	99.9	389,426	51,713
99-865	29	6572	258	111	0.06	69.959	99.8	508,706	94,889
99-869	81	15811	335	140	0.05	221.813	95.5	1,295,394	205,956
99-874	17	4395	96	146	0.03	123.812	95.4	526,085	84,107
99-883	29	7282	58	121	0.03	83.922	99.9	564,556	103,384
99-884	149	32501	115	98	0.04	174.997	99.9	1,164,992	341,468
99-889	31	6694	252	87	0.03	85.269	99.3	609,874	154,383

with their stalks. The batteries in four of the six tags, which were in fish at liberty for 175 days or more, failed and these tags stopped collecting data. Fortunately, however, previously collected data were preserved in the nonvolatile memories of the tags. Perhaps the most important feature of archival tags is their ability to collect data on the movement of tagged fish at frequent intervals from release until recapture (Hunter et al., 1986; Gunn and Block, 2001). There are, however, several factors that can affect the accuracy of the geoposition estimates. These include, but are not limited to, latitude, equinoxes, resolution of the light sensor, light attenuation, and behavior of the fish (Gunn and Block, 2001; Musyl et al., in press).

Gunn et al.[4] previously reported the accuracy of geolocation estimates from the light data from archival tags attached to southern bluefin tuna (*Thunnus maccoyii*) held in cages in the Indian Ocean to be about 0.5° in longitude and 1.5° in latitude. Welch and Eveson (1999) and Musyl et al. (2001) estimated the accuracy of geolocation estimates from the light-level data recorded by archival tags by comparing the known and estimated locations of tags that were attached to oceanographic buoys in the north Pacific. The reported accuracy by Welch and Eveson (1999) was ±0.9° in longitude and ±1.2° in latitude. The reported accuracy by Musyl et al. (2001) ranged from 0.2° to 0.3° in longitude and from 1.5° to 4.4° in latitude. In our study, we estimated the accuracy of geolocation estimates (longitude: 0.5°, latitude: 2.0°) by comparing the known and estimated locations of 21 bigeye tuna on their days of recapture (Table 3).

We used our estimates of accuracy and precision as criteria for filtering the daily geolocation estimates. In other studies where archival tags were used to provide estimated movement paths, geolocation estimates derived from light data have been verified or adjusted by comparing recorded temperatures from archival tags with maps of estimated sea-surface temperatures from satellite data (Gunn and Block, 2001). In the equatorial EPO, sea-sur-

[4] Gunn, J. S., T. W. Polacheck, T. L. O. Davis, M. Sherlock, and A. Betlehem. 1994. The development and use of archival tags for studying the migration, behavior and physiology of southern bluefin tuna, with an assessment of the potential for transfer of the technology to groundfish research. *In* Proceedings of ICES mini-symposium on fish migration, 23 p. International Council for the Exploration of the Sea, Palaegade 2-4, DK-1261 Copenhagen K, Denmark.

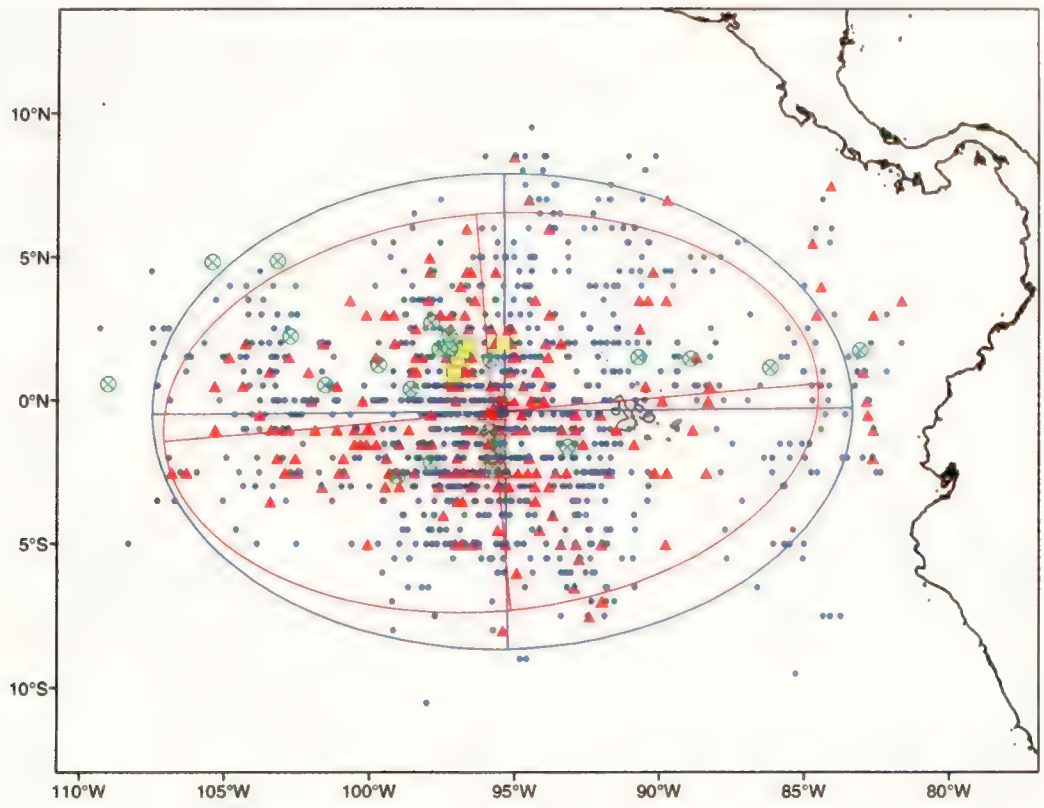

Figure 10

Geolocation estimates for 22 bigeye tuna at liberty for 30 d or longer (Table 4) classified as unassociated (blue dots) or associated with floating objects (red triangles). The yellow solid squares are the release locations and the green crosshairs are the recapture locations. The larger blue and red dots, axes, and elipses are the arithmetic means, major and minor axes, and 95% probability ellipses, respectively, for the spatial distributions of the geolocation estimates for unassociated behavior and behavior associated with floating objects.

face temperatures vary little over extremely large areas (Fiedler, 1992); therefore this technique is much less useful than in temperate regions.

The movement paths shown for bigeye tuna in our study (Figs. 9 and 10) derived from the filtered archival tag light data indicated that the area was restricted to the equatorial EPO. No fish traveled further west than about 110°W, and most movements were constrained between about 95° and 100°W and 3°N and 5°S. However, the value of the archival tags in providing fisheries-independent information on dispersion and movement paths is apparent, especially considering the fact that 16 of the fish were recaptured within 300 nmi of where they were released. Furthermore, the minimum convex polygon for the filtered archival tag data is approximately four times the area of the minimum convex polygon surrounding the release and recapture positions. Movements of bigeye tuna inferred from large-scale conventional tagging programs in the western Pacific (Hampton and Gunn, 1998; Hampton et al.[5]; Kaltongga[6]) and Hawaii (Itano and Holland, 2000) indicate that, although there are some long-distance movements, most recoveries are near their points of release. Those data appear to indicate, as do those of the present study, regional fidelity for bigeye tuna, and that the expected degree of mixing is quite low between the EPO and the central and western Pacific Ocean (CWPO).

The estimated mean velocity of 117 km/d or 2.6 knots (Table 4) is comparable to the estimate of 130 km/d for Pacific bluefin tuna (*Thunnus orientalis*) from archival tag data (Tsuji et al., 1999). Although this estimate should not be interpreted as actual swimming speed through the water, considering the imprecision of the movement paths and the fact that daily vertical movements were not

[5] Hampton, J., K. Bigelow, and M. Labelle. 1998. A summary of current information on the biology, fisheries and stock assessment of bigeye tuna (*Thunnus obesus*) in the Pacific Ocean, with recommendations for data requirements and future research. Secretariat of the Pacific Community, Oceanic Fisheries Programme, Technical Report 36,46 p. Oceanic Fisheries Programme, SPC, B.P. D5, 98848 Noumea Cedex, New Caledonia.

[6] Kaltongga, B. 1998. Regional tuna tagging project: data summary. Oceanic Fish. Prog. Tech. Rept. 35, 70 p. Secretariat of the Pacific Community. Noumea, New Caledonia. Oceanic Fisheries Programme, SPC, B.P. D5, 98848 Noumea Cedex, New Caledonia.

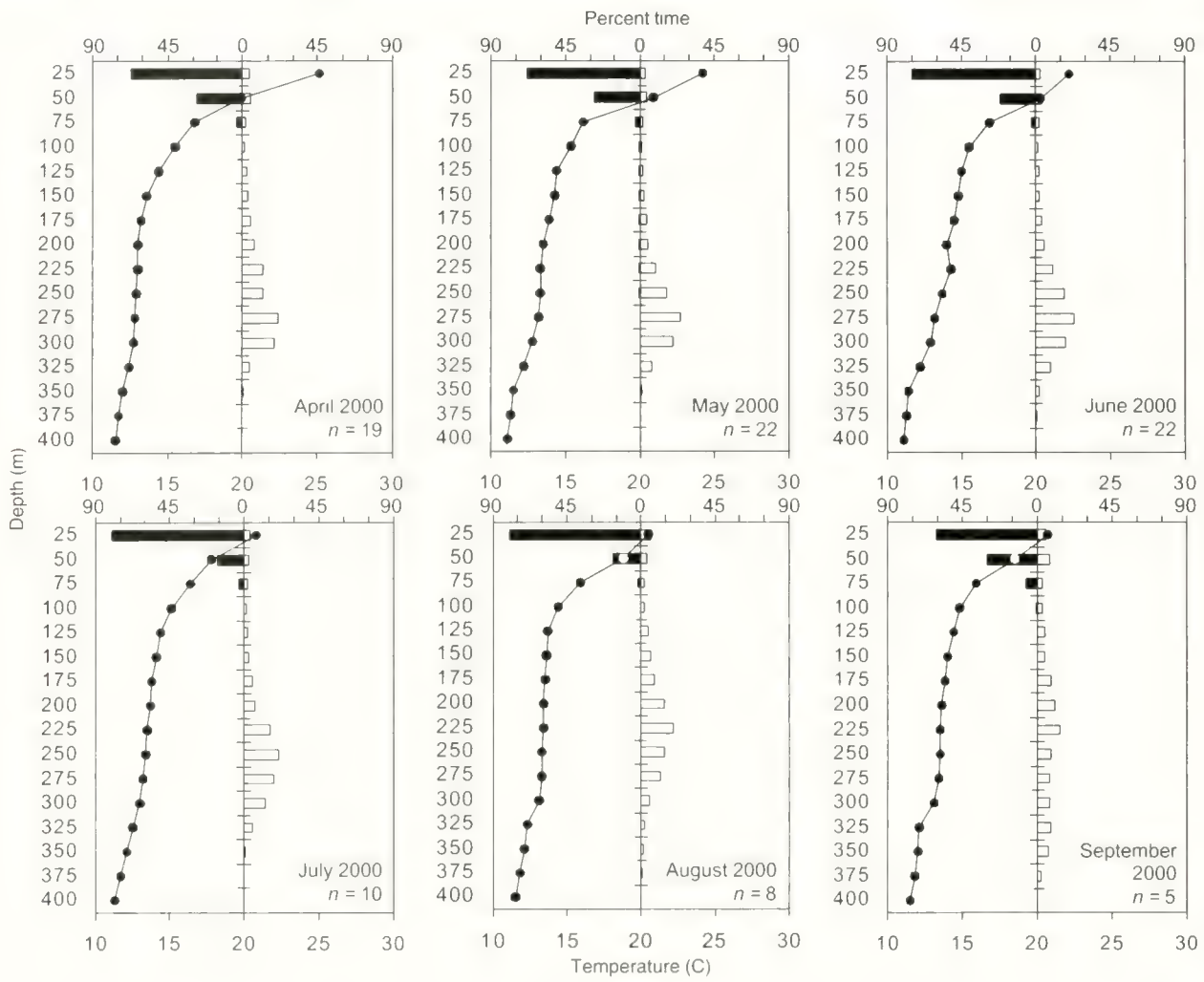

Figure 11

Depth frequencies of bigeye tuna during the night (solid bars) and day (open bars), along with the vertical thermal profiles by month and year (unassociated type-1 behavior days only). Data from depths greater than 400 m are excluded. The number of fish represented in each month is given.

included in the calculations of velocity. Nevertheless, this estimate should be useful for incorporation into a spatially stratified movement model that is designed to evaluate dispersion and mixing rates between large regions (see Sibert and Fournier, 2001).

Sonic tracking studies have shown that the diel vertical migrations of bigeye tuna are closely associated with vertical movements of organisms of the deep scattering layer (DSL). Bigeye tuna probably forage on squids and other mesopelagic organisms within the DSL throughout the day and night (Josse et al., 1998; Dagorn et al., 2000). As reported by Blunt (1960), squid are very important in the diet of subsurface bigeye tuna, in the eastern tropical Pacific (ETP)—70% of the stomachs examined contained squid equivalent to 60% of the total food volume. Fiedler et al. (1998) reported the depths of the DSL in the ETP as 300–400 m during the day and 0–100 m at night. Other studies have documented that bigeye tuna have evolved anatomical and physiological adaptations to enable them to exploit organisms of the DSL during the daytime in a dark, cold, and oxygen-poor environment (Kawamura et al., 1981; Holland et al., 1992; Brill, 1994; Holland and Sibert, 1994; Schaefer, 1999; Lowe et al., 2000; Graham and Dickson, 2001).

The depth distributions of bigeye tuna not associated with FADs near Hawaii and in the Coral Sea are significantly greater than those for bigeye tuna in the equatorial EPO. It seems possible that the greater daytime depths exhibited by bigeye tuna in the CWPO are related to the greater daytime DSL depths (≥400 m) in that region (Maynard et al., 1975; Tont, 1976; Davies, 1977; Kuznetsov et al., 1982; Fiedler et al., 1998; Josse et al., 1998). For a 112-cm

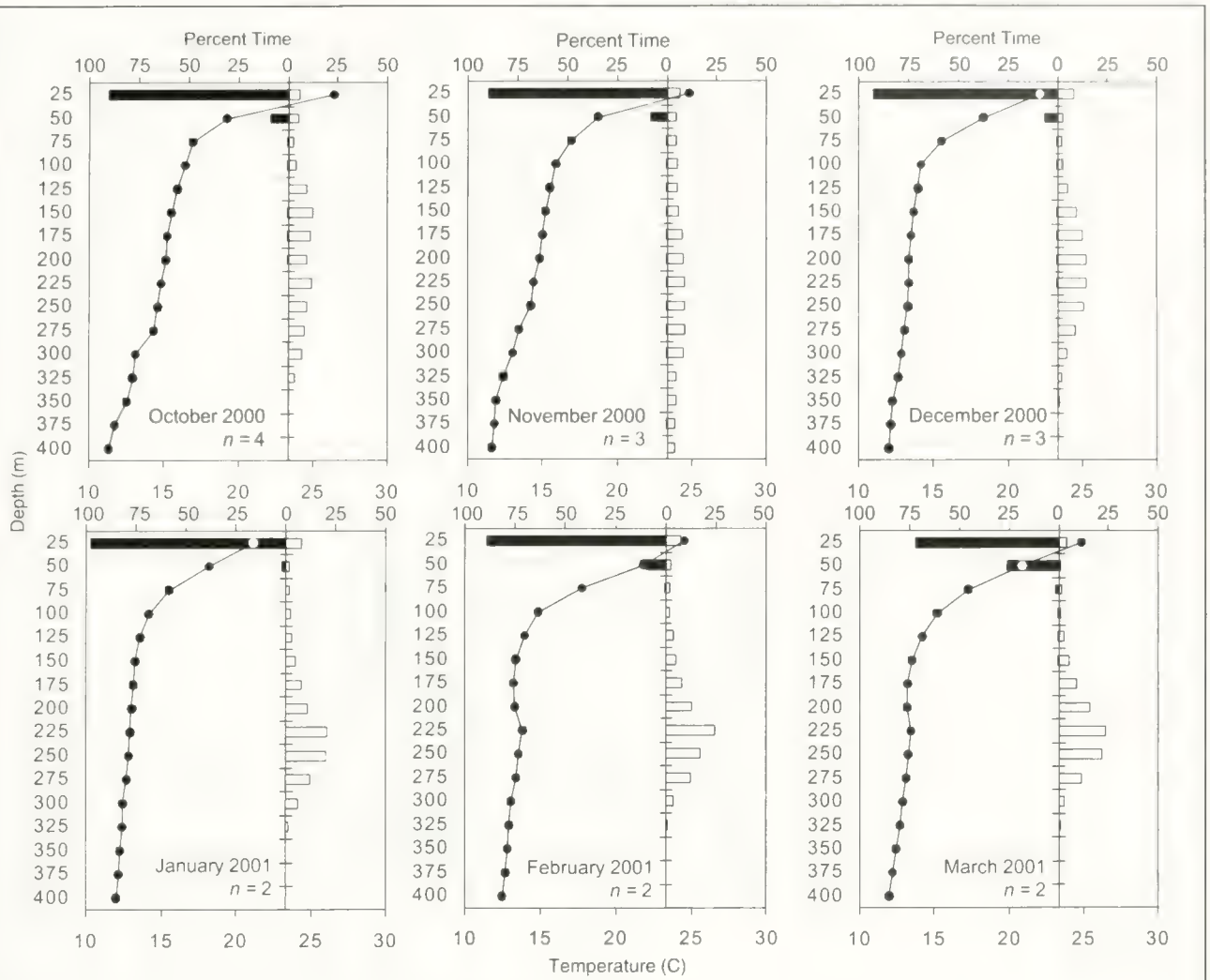

Figure 11 (continued)

bigeye tuna in the equatorial EPO not associated with a FAD (Fig. 2), the baseline daytime depth was 250 to 300 m at temperatures of 12° to 13°C. For a 131-cm bigeye tuna exhibiting similar behavior in Hawaiian waters, the baseline daytime depth was 400 to 500 m at temperatures of 7° to 10°C (Musyl et al., in press). Gunn and Block (2001) reported that bigeye tuna with archival tags in the Coral Sea showed that the mean depth of the fish at night was 50 m and that during the day they were at depths of 450 to 500 m and at temperatures of 7° to 9°C.

The average light level experienced by bigeye tuna at night (77 Wildlife Computer's light level [wcl] at 24 m), is below that experienced during the day (126 wcl at 242 m). Therefore, bigeye tuna do not occupy an isolume as has been suggested for other vertically migrating organisms (Widder and Frank, 2001). Bigeye tuna are also able to adapt to much higher light levels (195 wcl) for prolonged periods when remaining at shallow depths during daylight hours when they are associated with FADs.

Unassociated type-2 behavior observed in bigeye tuna (Fig. 5 and Table 2) may be attributed to a shift in the vertical distribution of prey items. Monospecific 100- to 200-ton schools of bigeye tuna (>100 cm length) were observed feeding at the surface on the mesopelagic fish *Vinciguerria lucetia* during daylight hours on 15 December 1978 in the equatorial EPO (K. Schaefer, unpubl. data). *Vinciguerria lucetia* is normally distributed at depths of 500 m or more during the day and is common in the 0–90 m layer at night (Blackburn, 1968). During the 1971–91 period, previous to the development of the drifting FAD fishery in the EPO, many purse-seine sets made during daylight hours were successful in capturing bigeye tuna schools not associated with drifting objects (Calkins et al., 1993). Atypical behavior of large schools of *Vinciguerria nimbari*, present in large concentrations within the mixed layer during the day, has also been observed in the equatorial Atlantic Ocean (Marchal and Lebourges, 1996). This type of behavior has also been observed in the Coral Sea, where bigeye

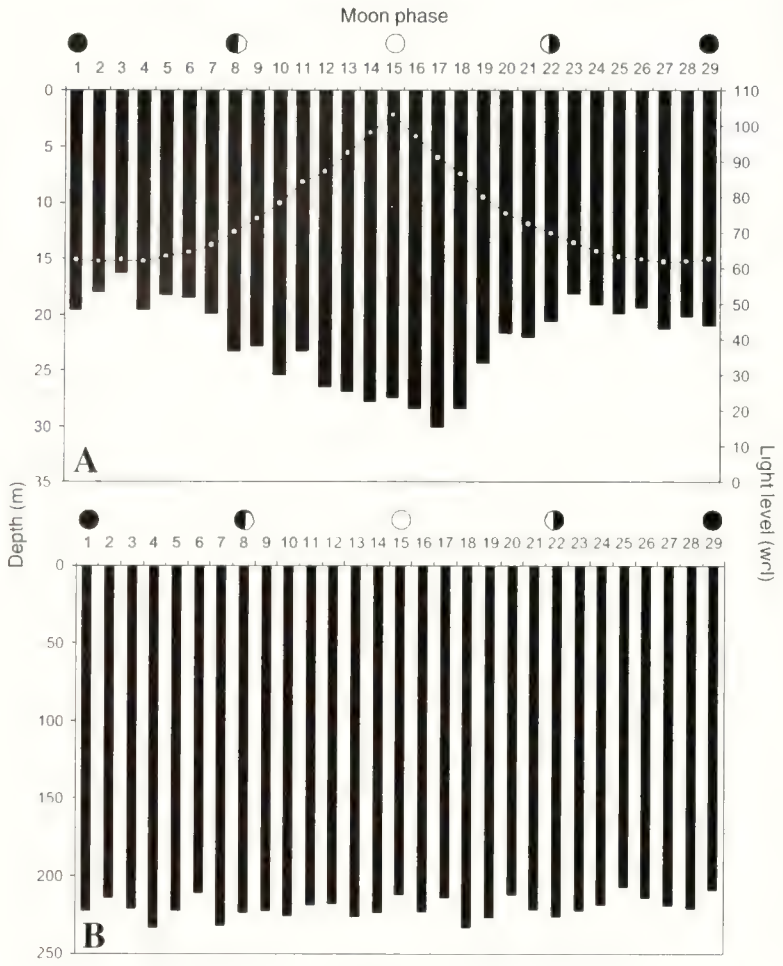

Figure 12

Average (**A**) nighttime and (**B**) daytime depths (solid bars) and light levels (open circles) for 22 bigeye tuna, by moon phase (unassociated type-1 behavior days only).

tuna are caught throughout the day near the surface by both handline and longline fisheries between October and December (Hisada, 1973). A second explanation for some of the unassociated type-2 behavior is that the fish were still possibly associated with a FAD but were making afternoon excursions into the DSL, foraging for food.

Occasionally bigeye tuna make dives in excess of 500 m (Fig. 7 and Table 2). The durations of the deep diving events are not correlated (r=0.0008, P>0.05) with body size. Moreover, there appear to be two types of deep dives (Table 2). One may be for predator avoidance. The fish descend and then ascend rapidly back to the depth at which it had been previous to the dive. The second type may be a foraging behavior, where prolonged time is spent at greater depths, up to 1000 m. Deep dives to 1000 m or more have also been reported from archival tag data for bigeye tuna in the Coral Sea (Gunn and Block, 2001) and for Atlantic bluefin tuna (Block et al., 2001a; Block et al., 2001b).

Bigeye tuna exhibiting behavior associated with floating objects (Fig. 6 and Table 2) generally remain above the thermocline, but they still show a diel shift in depth distribution. They remain at about 6 m, on average, deeper during the day than at night (Fig. 6). Stomach content analysis of FAD-associated bigeye tuna in the eastern Atlantic Ocean by Ménard et al. (2000) showed that 82.7% of the stomachs were empty, where as only 25% of the stomachs of bigeye tuna unassociated with floating objects were empty. They concluded that FADs do not have a trophic function. However, the observed excursions to depths of about 300 m for a few hours at about 1800 h for four consecutive days by a FAD-associated bigeye tuna (Fig. 1B) may be related to foraging for prey in association with the DSL.

Parin and Fedoryako (1999) stated that tunas associate with floating objects only temporarily because there are insufficient food resources in the vicinity of these devices. We found that residence times and total times spent at FADs are limited (Table 2). Our observations do not support the

hypothesis of Marsac et al. (2000) that association with FADs causes bigeye tuna to be retained within areas or transported to new areas, thus creating an ecological trap. An alternative hypothesis, suggested by Hunter and Mitchell (1966), is that FADs function by simply providing a visual stimulus in an optically void environment. An extension of their hypothesis should include the fact that FADs provide a general sensory stimulus, including sound produced by the FAD and associated fauna, which may be the mechanism by which tunas locate FADs. In addition to a general sensory stimulus, FADs may also function as reference points (Freon and Dagorn, 2000).

Archival tags have provided data on the type of habitat selected (light levels, depths, and temperatures) that should be useful for standardizing the catch per unit of effort (CPUE) of bigeye tuna by surface and longline fisheries in the EPO. The data in Table 5 indicate that bigeye tuna greater than 110 cm spend 87% or more of their time above 50 m, in the mixed layer at night and 53% or more of their time between 200 and 300 m during the day. Habitat-based stock assessment models (Hinton and Nikano, 1996; Hinton and Deriso, 1998; Hampton et al.[1]) have been developed for the integration of data, such as those provided in Table 5, to adjust effort based on estimated fishing depth of longline gear (Mizuno et al., 1999) in relation to the vertical distribution of target species by time of day. The fishing depth of longline gear has been shown to be an important source of variation in the CPUE for bigeye tuna (Hanamoto, 1987; Boggs, 1992); higher catch rates of bigeye tuna have been associated with greater fishing depths of the longline gear. This has been interpreted previously as a preference of bigeye tuna for 10° to 15°C water during daylight hours (Hanamoto, 1987; Holland et al., 1990; Boggs, 1992; Brill, 1994).

We suggest that bigeye tuna are most likely not selecting their daytime and nighttime habitats based on temperature, depth, or light preferences, but on the distributions of their preferred prey. Cephalopods and mesopelagic fishes also show diel vertical migrations (as do other organisms) associated with the DSL. We suggest that the depths and temperatures preferred by bigeye tuna during daylight hours when exhibiting unassociated type-1 behavior are the environmental variables associated with their preferred prey.

The greater depths and lower temperatures at which bigeye tuna are caught during the daytime in the CWPO (Hampton et al.[5]; Miyabe[7]) may be a function of the greater daytime depths of the DSL

Table 5

The percentages of time 13 bigeye tuna (greater than 110 cm) spent within depth intervals by time of day (unassociated type-1 behavior days only). (CTZ = central time zone.

Depth (m)	Hour (CTZ)																							
	0000	0100	0200	0300	0400	0500	0600	0700	0800	0900	1000	1100	1200	1300	1400	1500	1600	1700	1800	1900	2000	2100	2200	2300
0–25	73.4	73.0	73.0	73.9	72.6	44.0	3.6	2.2	2.5	2.8	3.1	2.9	3.2	3.0	3.0	2.9	2.8	2.3	17.3	63.2	72.6	72.0	71.7	72.6
26–50	21.9	22.0	22.2	21.9	23.4	26.7	5.7	2.4	2.9	3.0	2.9	3.1	2.7	2.8	2.8	2.7	2.5	2.1	12.0	25.2	23.7	23.5	23.4	22.7
51–75	3.1	3.1	3.3	2.7	2.9	8.3	3.4	1.0	1.0	1.1	1.2	0.9	1.1	0.9	0.9	1.1	1.0	1.1	6.6	4.5	2.7	3.3	3.8	3.3
76–100	0.5	0.4	0.5	0.5	0.4	4.5	2.8	0.8	0.9	0.8	0.7	0.7	0.7	0.8	0.7	0.6	0.8	1.2	3.6	1.2	0.4	0.3	0.4	0.6
101–125	0.2	0.3	0.3	0.2	0.2	4.2	5.1	2.6	1.9	1.3	1.6	1.2	1.3	1.3	1.5	1.6	1.7	2.1	4.9	1.1	0.2	0.2	0.1	0.1
126–150	0.2	0.3	0.2	0.2	0.2	3.3	6.3	3.9	3.1	2.4	2.5	2.3	2.3	2.7	2.5	2.9	3.1	3.5	5.7	1.0	0.2	0.2	0.1	0.2
151–175	0.2	0.2	0.1	0.2	0.2	2.7	8.8	5.4	5.1	4.7	4.7	4.6	4.0	4.8	5.3	5.0	4.6	5.0	6.7	1.1	0.1	0.1	0.2	0.1
176–200	0.2	0.1	0.1	0.1	0.1	2.1	10.8	7.1	7.6	7.4	7.1	7.1	7.1	6.5	6.4	6.8	6.5	7.1	8.0	1.0	0.1	0.2	0.1	0.1
201–225	0.2	0.2	0.1	0.1	0.1	1.9	16.9	11.7	12.1	12.9	12.7	12.9	13.4	13.0	13.3	12.0	11.9	12.1	12.9	0.8	0.1	0.1	0.1	0.1
226–250	0.1	0.1	0.1	0.1	0.1	1.1	17.2	17.3	13.9	14.5	15.0	15.8	16.7	15.7	15.4	15.0	14.8	19.0	12.1	0.4		0.1	0.1	0.1
251–275		0.2	0.1			0.8	12.5	24.5	21.2	19.6	19.6	19.3	18.4	19.1	19.0	19.4	22.3	26.1	7.0	0.2			0.1	
276–300				0.1		0.4	5.1	16.3	19.5	18.8	17.9	17.8	17.7	18.1	18.5	19.7	19.8	14.0	2.4	0.1				
301–325						0.1	1.7	3.9	7.1	8.6	8.5	8.3	8.5	8.8	8.4	8.7	6.8	3.9	0.7	0.1				
326–350							0.2	0.9	1.2	1.5	2.0	2.3	2.5	2.0	1.8	1.4	1.2	0.5	0.1					
351–375								0.1	0.1	0.3	0.4	0.6	0.4	0.5	0.4	0.3	0.1							
376–400											0.1	0.1		0.1	0.1									

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in those regions, compared to the daytime depths of the equatorial EPO (Maynard et al., 1975; Tont, 1976; Davies, 1977; Kuznetsov et al., 1982; Fiedler et al., 1998; Josse et al., 1998). Farr and Best (1998) reported that DSL distributions are related to mesoscale oceanographic features, defined by flow and temperature variability, and are most commonly observed at the pycnocline.

Geographic variation in DSL depths throughout the Pacific are possibly related to isolumes of the associated micronekton, and can potentially be estimated from the light level data recorded by the archival tags attached to bigeye tuna. Variation in daytime DSL depths is probably a function of light penetration (which is regulated by biological production) and absorption of light by chlorophyll and phaeopigments (Tont, 1976).

The behavior of bigeye tuna is strongly influenced by the presence of drifting FADs within their habitat. Because of this behavior associated with FADs, even though it is for relatively short periods, bigeye tuna are highly vulnerable to capture by purse-seine vessels. Estimates of bigeye tuna residence times and percentages of total time associated with drifting FADs, along with estimates of FAD densities, could be used to evaluate vulnerability to capture by the surface fishery. There is a critical need for conducting a large-scale tagging program in the EPO focused on bigeye tuna—a program where conventional tags are used for estimating size-specific mortality and mixing rates and archival tags are used for evaluating fine-scale movements, behavior, and habitat selection.

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An evaluation of back-calculation methodology using simulated otolith data

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Abstract—I simulated somatic growth and accompanying otolith growth using an individual-based bioenergetics model in order to examine the performance of several back-calculation methods. Four shapes of otolith radius-total length relations (OR-TL) were simulated. Ten different back-calculation equations, two different regression models of radius-length, and two schemes of annulus selection were examined for a total of 20 different methods to estimate size at age from simulated data sets of length and annulus measurements. The accuracy of each of the twenty methods was evaluated by comparing the back-calculated length-at-age and the true length-at-age. The best back-calculation technique was directly related to how well the OR-TL model fitted. When the OR-TL was sigmoid shaped and all annuli were used, employing a least-squares linear regression coupled with a log-transformed Lee back-calculation equation (y-intercept corrected) resulted in the least error; when only the last annulus was used, employing a direct proportionality back-calculation equation resulted in the least error. When the OR-TL was linear, employing a functional regression coupled with the Lee back-calculation equation resulted in the least error when all annuli were used, and also when only the last annulus was used. If the OR-TL was exponentially shaped, direct substitution into the fitted quadratic equation resulted in the least error when all annuli were used, and when only the last annulus was used. Finally, an asymptotically shaped OR-TL was best modeled by the individually corrected Weibull cumulative distribution function when all annuli were used, and when only the last annulus was used.

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The average rate of growth of an individual fish in a population is critical to age-based stock assessments. The average rate at which the fish within the stock increases in weight ultimately determines the level of effort required to extract a desired yield from the stock as a whole (Ricker, 1975). Furthermore, current conservation standards (Gulland and Boerema, 1973; Goodyear, 1993) are dependent upon the rate of individual growth. Thus, errors in the estimation of growth can lead to erroneous advice to fishery managers concerning the present and possible future status of a population.

By far the most common method of estimating fish growth rate is by estimating the age of individual fish from calcified structures (scales, otoliths, spines, etc.; but for this study, however, otoliths were considered the representative hard structure) and with the subsequent assumption that these fish are an unbiased representation of size at that age. Growth is then described as the change in weight or length over some unit of time. To standardize age at which size is estimated, or to obtain length-at-age data on ages not included in the sample, back-calculation techniques are often employed to estimate a fish's size at a previous age (Bagenal, 1978). The process of back calculation can be broken down into three steps: verification of the periodicity of annulus formation, establishment of an otolith radius-total body length (OR-TL) relation, and the estimation of size at the time of annulus formation. In this study, I used simulations to examine how the establishment of the OR-TL relation and the form of the back-calculation equation used may influence growth rate estimates made from otoliths.

The back-calculation process assumes that somatic growth is directly related to otolith growth (Bagenal, 1978). This assumption is usually validated through the demonstration of a relationship between the otolith radius and body length by a least-squares regression of body length on otolith radius. A variation of this technique uses a functional (model II) regression, based on the assertion that neither body length nor otolith radius are truly independent (i.e. measured without error) (Ricker, 1973, Laws and Archie, 1981). Uncertainties can enter this process from several sources. For example, incomplete data can make it difficult to discern if this relationship is linear. Furthermore, using regression to estimate beyond the range of the data is not recommended. Estimating beyond the range of the data can become a problem when back-calculating to very early ages that are not represented in the sample. Furthermore, several studies have found that otolith growth and somatic growth can be uncoupled (Mosegaard et al., 1988; Reznick et al., 1989; Secor and Dean, 1989; Wright et al., 1990; Milicich and Choat, 1992; Secor and Dean, 1992). Hales and Able (1995) found that changes in somatic growth accounted for only half of the variation in otolith growth. This uncoupling of somatic and otolith growth rates challenges the assumption that back-calculation is based on.

The question of what is the proper back-calculation equation to use is a question that has received considerable attention. Bagenal (1978) discussed three separate methods and suggested that a combination of methods might be helpful in some cases. Francis (1990) presented an in-depth review of

six different back-calculation equations and their use. Ricker (1992) later commented on the conclusions of Francis (1990) to suggest yet another variation on the method. Further variation exists on exactly which combination of annuli to use. Standard method suggests the use of all available annuli within the otolith to increase sample size. However, recent literature (Vaughan and Burton, 1994), as well as older reports (Ricker, 1973), have suggested that only the most recently formed annuli should be used. A review of the literature on age and growth shows that a variety of techniques are in use today and that there is no real agreement on a definitive method. The purpose of this study was to examine how well the various back-calculation techniques accurately estimate lengths at previous ages and to examine the biases associated with each technique.

Methods

Model structure

I simulated somatic and otolith growth using a bioenergetics model. A detailed description of the model is presented in Schirripa and Goodyear (1997). The life history and growth parameters were calibrated to fit, as closely as possible, to reported estimates of striped bass growth (Bason[1]); however the model is not intended to be a striped bass model *per se*. Because of the commercial and recreational importance of striped bass, a great body of literature from the field and laboratory work is available. One of the most studied populations of striped bass is that of the Chesapeake Bay system (Cohen et al., 1983; Coutant et al., 1984; Goodyear, 1984, 1985; Tuncer, 1988; Coutant and Benson, 1990; Secor, 1992; Brandt and Kirsch, 1993; Rose and Cowan, 1993; Rutherford and Houde, 1995; Secor and Houde, 1995). Biological and environmental parameters reported for the populations of this system were used whenever possible. The growth model used an individually based framework, but rather than following every fish of the cohort singly, "cells" of fish with identical attributes were followed instead (Rose et al., 1993). A total of 250 cells, each with eleven attributes, were modeled. Attributes examined included age, length, biomass, daily food ration, food conversion efficiency, otolith weight, otolith radius, maximum length attained, maximum biomass attained, brain weight, condition factor, and number of fish that the cell represented.

The term "population" is used to define those fish that remained alive for the entire simulation, unaffected by either natural or fishing mortality. The term "catch" refers to the entire group of fish that were susceptible and killed due to fishing mortality, and "sample" refers to a subsample of individuals from the catch, selected on the basis of length and frequency within the catch. Frequency in the catch was a function of the selectivity of the gear under consideration and frequency in the population. For the purposes of this study, gear was considered nonselective. Annulus formation within the otolith was assumed to occur at the end of every growth year and to be measured without error.

The specific somatic growth rate of an individual fish was calculated by a balanced energy equation. Equations for rates of consumption, respiration, egestion, and excretion generally followed those given by Hewett and Johnson.[2] The otolith growth model used was a modification of the equations presented by Mosegaard.[3] Fish formed an otolith when they reached 90 mm in length. Daily change in otolith weight (O_w) was modeled as a function of daily change in either brain weight (B_w) or brain length (B_l). In the case of brain weight, weight specific brain growth rate was modeled as a function of the somatic growth rate as follows

$$Growth.Brain = Growth.Somatic \times a_2, \quad (1)$$

where a_2 = less than 1, denoting that brain growth rate is slower than somatic growth rate.

The change in B_W then was calculated as

$$dB_w/dt = Growth.Brain \times B_W. \quad (2)$$

The daily change in otolith weight was then calculated as

$$dO_W/dt = a_4 \times Brain.weight \times temp^{a_1}, \quad (3)$$

where a_4 = the conversion factor from brain weight to otolith weight (see below);
$temp$ = the average temperature for the day in degrees centigrade; and
a_1 = 0.77, which is used to determine the overall size of the otolith.

Otolith radius, O_r, was then calculated from O_w assuming a spherical shape as

$$O_r = \frac{O_W}{SpD} \times (3/4\pi)^{0.333}, \quad (4)$$

where SpD = 2.5 and is the specific density of the otolith.

Assuming a spherical shape resulted in a unique radius for a given weight (i.e. a sphere made it unnecessary to consider otolith length).

When brain length was used to model otolith radius, B_w was calculated as in Equation 2 and B_l was calculated as the cube root of B_w:

[1] Bason, W. H., S. E. Allison, L. O. Horseman, W. H. Keirsey, P. E. LaCivita, R. D. Sander, and C. A. Shirey. 1976. Ecological studies in the vicinity of the proposed Summit Power Station January through December 1975. Vol. 1, Fishes, 392 p. Ichthyological Associates, Ithaca, NY.

[2] Hewett, S. W., and B. L. Johnson. 1992. Fish bioenergetics model 2. Sea Grant Institute, Technical Report WIS-SG-92-250, 79 p. University of Wisconsin, Madison, WI.

[3] Mosegaard, H. 1994. A model of otolith and larval fish growth. *In* ICES, Report of the working group on recruitment processes, C.M. 1994/L:12, p. 34–38.

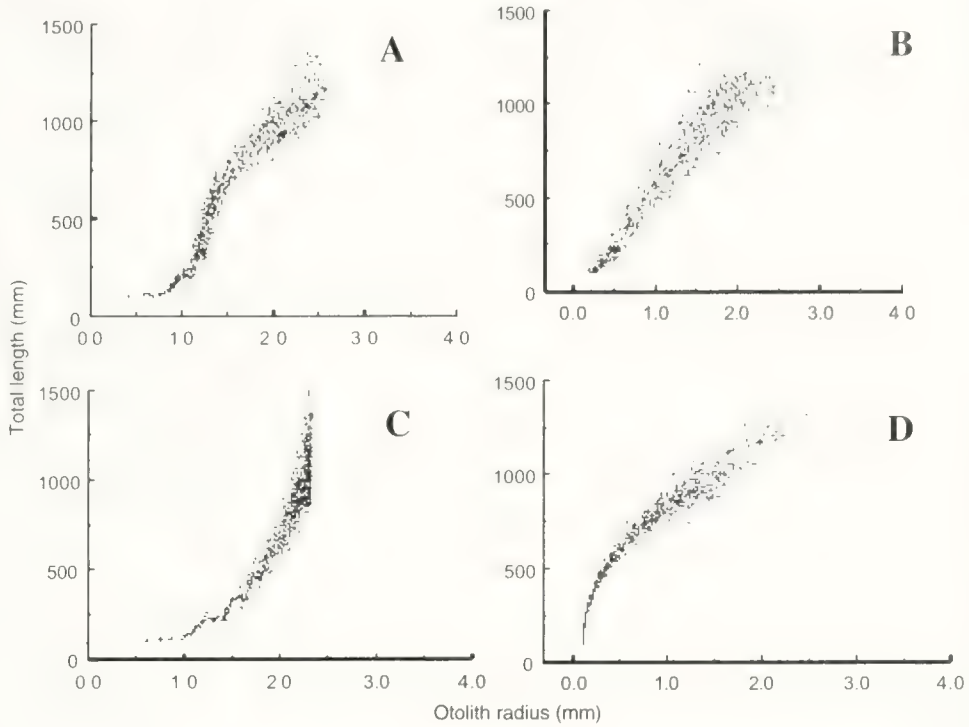

Figure 1

Scatter plot of the four simulated otolith radius-total length relations (OR-TLs). (**A**) OR-TL/SIG = sigmoid shaped; (**B**) OR-TL/LIN = linear shaped; (**C**) OR-TL/EXP = exponentially shaped; (**D**) OR-TL/ASYM = asymptotically shaped.

$$B_1 = B_W^{0.333}. \quad (5)$$

O_r was then calculated as

$$O_r = B_1 \times 0.5. \quad (6)$$

Otolith radius-total length relation

The OR-TL relation was fitted as closely as possible to that reported for striped bass by Heidinger and Clodfelter (1987). Modeling the conversion factor a_4 (Eq. 3) as a function enabled me to generate four different OR-TL relations typically found in nature. A sigmoid shaped OR-TL (OR-TL/SIG) relation (Fig. 1A) relation was achieved by setting the parameter $a_2 = 0.08$ and modeling the parameter a_4 as a function of body length:

$$a_4 = 9 + (-7 \times \mathrm{Sin}(0.006 \times Length) + 5). \quad (7)$$

A linear shaped OR-TL (OR-TL/LIN) relation (Fig. 1B), as found in striped bass (Heidinger and Clodfelter, 1987) was achieved by setting the parameter a_2 (from Eq. 1) to 0.85 and modeling otolith radius as a function of brain length (the parameter a_4 was not necessary for this relation). An exponential OR-TL(OR-TL/EXP) relation (Fig. 1C), similar to that found for vermilion snapper, *Rhomboplites aurorubens*, (Grimes, 1978) was achieved by again setting the parameter a_2 to 0.08 and modeling the parameter a_4 as a linear function of otolith weight:

$$a_4 = 25 - (1.75 \times O_W). \quad (8)$$

An asymptotic OR-TL (OR-TL/ASYM) relation (Fig. 1D), similar to that found for walleye, *Stizostedion vitreum*, (Heidinger and Clodfelter, 1987), was achieved by keeping the parameter $a_2 = 0.08$ and modeling the parameter a_4 as a function of total length:

$$a_4 = 8.717E - 12 \times Length^4. \quad (9)$$

Mortality

Mortality could occur from three sources: direct starvation, random natural mortality based on length, and fishing mortality. If a fish lost more than a specified percentage of its maximum attained body weight (35% for larvae and 50% for juveniles), it died from starvation. Fishing mortality was described first as an overall value (F=0.4) and then divided by 365 to calculate a daily value. In order to ensure that there would be no sampling bias due to gear selectivity, fishing mortality was assumed to be nonselective (random).

The four simulated OR-TL relations were described by using four different functions: 1) ordinary least squares (OLS) linear regression (model I)

Table 1

The ten back-calculation and OR-TL regression equations evaluated in this study. Method number refers to all annulus/last annulus only. L_n is the estimated length at formation of annulus R_n; L_c and R_c is total length of fish and otolith radius at capture, respectively. OLS = ordinary least squares.

Method	Back-calculation equation	OR-TL fitting method
1/11	$L_n = (R_n / R_c) L_c$	none
2/12	$L_n = a + (bR_n)$	OLS linear regression
3/13	$L_n = a + (R_n / R_c)(L_c - a)$	OLS linear regression
4/14	$L_n = a + (bR_n)$	functional linear regression
5/15	$L_n = a + (R_n / R_c)(L_c - a)$	functional linear regression
6/16	$\log_e(L_n) = \log_e(a) + b(\log_e(R_n))$	OLS linear regression with log transformation
7/17	$\log_e(L_n) = \log_e(L_c) + b(\log_e(R_n) - \log_e(R_c))$	OLS linear regression with log transformation
8/18	$L_n = K(1 - \exp(-(R_n / \alpha)^\beta))$	Weibull cumulative function
9/19	$L_n = c + (dR_n) + (eR_n^2) + (fR_n^3)$	quadratic equation
10/20	$L_n = (K(L_c / L_p))(1 - \exp(-(R_n / \alpha)^\beta))$	Weibull cumulative function

$$L_c = a + R_c b, \tag{10}$$

where L = the total length; and R = the otolith radius and represents the independent variable (assumed to be measured with out error); 2) functional regression (model II), which has the identical formula as Equation 10 but does not assume an independent variable (i.e. both L and R are measured with error); 3) Weibull cumulative function (Weibull, 1951),

$$L_n = K\left(1 - \exp\left[-\left(\frac{R}{\alpha}\right)^\beta\right]\right), \tag{11}$$

and 4) a third order quadratic equation

$$L_n = c + (d_1 R_n) + (e_2 R_n^2) + (f_3 R_n^3). \tag{12}$$

These four functions were fitted with the SAS NLIN procedure (SAS, 1988).

Ten combinations of the back-calculation formula and OR-TL fitting procedures were used (Table 1). Methods 1 through 9 were simple derivations from a standard regression equation and required only a fitting of the parameters and substitution into the equation (Bagenal, 1978). Method 10 however used a derivation of the Weibull distribution function. In this method, the parameter defining the asymptotic limit of the function (K) was modified by L_c/L_p as

$$L_n = \left(K(L_c / L_p)\right)\left(1 - \exp\left[-\left(\frac{R_c}{\alpha}\right)^\beta\right]\right), \tag{13}$$

where L_p = the theoretical length of the fish according to its otolith radius as predicted by the fitted OR-TL Weibull function; and
L_c = the actual length at capture.

If, for instance, the actual length of the fish was less than the theoretical length (L_c/L_p is less than 1), the parameter

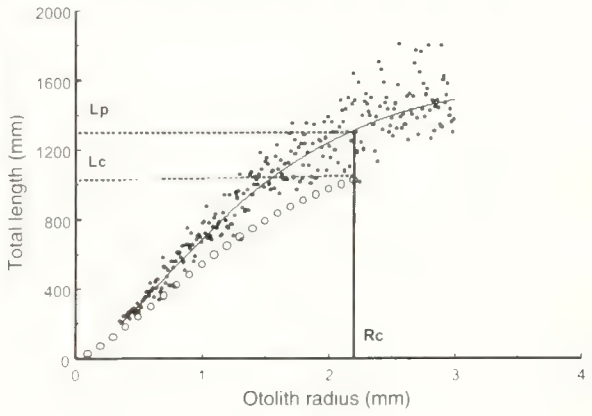

Figure 2

Demonstration of the individually corrected Weibull cumulative distribution function. The curve is the fitted equation to all data, Rc = otolith radius at capture, Lc = total length at capture, and Lp = total length predicted from Rc and the fitted curve. The asymptote parameter of the fitted equation (K) is multiplied by Lc/Lp to arrive at that fish's particular trajectory, denoted by the large empty circles.

K was corrected downward and subsequent back-calculations for that fish were made according to its own individual trajectory (Fig. 2). In this way, L_c/L_p was calculated for each individual fish in the same way that the slope of the Fraser-Lee back-calculation equation was estimated for each fish. These ten combinations were used for all available annuli and then repeated by using the last annulus only, for a total of twenty different methods.

As a measure of bias, the back-calculated length at age 2 was regressed on the age of the fish from which the estimate came (source age). In this way, for instance, a strong "Lee's phenomenon" (the phenomenon that back-calculated lengths for a given age group become smaller as

Table 2

Age (yr)	1	2	3	4	5	6	7	8	9	10	11	12	13	14	*n*
Age and calculated true mean length-at-age (mm) for a typical simulated population.															
1	102	—	—	—	—	—	—	—	—	—	—	—	—	—	250
2	108	208	—	—	—	—	—	—	—	—	—	—	—	—	250
3	108	208	330	—	—	—	—	—	—	—	—	—	—	—	250
4	108	208	329	457	—	—	—	—	—	—	—	—	—	—	250
5	107	207	329	457	573	—	—	—	—	—	—	—	—	—	250
6	107	207	329	457	572	674	—	—	—	—	—	—	—	—	250
7	107	207	329	457	572	674	763	—	—	—	—	—	—	—	250
8	108	207	329	457	574	676	766	845	—	—	—	—	—	—	250
9	108	208	330	459	576	679	769	849	917	—	—	—	—	—	250
10	108	208	330	460	578	681	772	853	921	980	—	—	—	—	250
11	108	208	331	460	577	680	771	852	920	981	1032	—	—	—	250
12	108	208	331	460	577	680	771	851	920	980	1031	1077	—	—	250
13	109	208	331	460	578	681	772	853	920	980	1031	1076	1115	—	250
14	109	208	331	459	577	678	769	849	916	974	1025	1070	1108	1139	250
Mean	104	208	330	458	575	677	768	850	918	978	1029	1073	1110	1138	
Age and calculated true mean length-at-age (mm) for a typical simulated catch.															
1	102	—	—	—	—	—	—	—	—	—	—	—	—	—	117
2	109	207	—	—	—	—	—	—	—	—	—	—	—	—	105
3	108	207	323	—	—	—	—	—	—	—	—	—	—	—	101
4	108	208	323	448	—	—	—	—	—	—	—	—	—	—	86
5	108	205	321	449	572	—	—	—	—	—	—	—	—	—	93
6	107	205	319	445	567	673	—	—	—	—	—	—	—	—	95
7	108	206	323	448	569	676	765	—	—	—	—	—	—	—	98
8	107	206	322	450	572	680	771	853	—	—	—	—	—	—	104
9	108	207	323	449	571	679	771	853	918	—	—	—	—	—	115
10	108	205	318	443	562	665	755	834	901	962	—	—	—	—	105
11	109	206	320	442	561	667	757	836	903	964	1016	—	—	—	106
12	107	204	316	438	557	661	751	831	901	964	1017	1060	—	—	102
13	107	204	315	439	559	664	756	838	908	973	1027	1071	1107	—	101
14	108	203	316	442	563	670	763	844	910	970	1021	1061	1096	1127	88
Mean	106	206	321	446	567	672	763	843	908	966	1020	1064	1102	1127	

the fish from which they are calculated become older) or a similar effect would result in a negative slope. If there is no bias caused by this approach, the expected value of this slope is zero when randomly sampled from an unfished population.

The accuracy of each of the twenty methods of back-calculation was evaluated by plotting the percent error of the estimated length-at-age in relation to the true value. As an overall evaluation of the method, a sum-of-squares (SS) was calculated by squaring the percent error between the estimated length-at-age and the true length-at-age and summing across all ages.

Results

The true underlying mean length-at-age of both the surviving population and the catch (Table 2) was calculated and tabulated in standard back-calculation type tables. There was no apparent trend in the estimates as a function of the age used in the back-calculation. This lack of trend, and the high degree of similarity between the mean length-at-age of the population and catch suggested that the catch was a random and representative sample of the population.

Methods 2, 4, 6, 8, and 9 resulted in the least bias and method 1 the most bias when the slopes were examined across the various shapes of the OR-TL relation (Fig. 3). The linear shaped OR-TL (OR-TL/LIN) relation resulted in the least amount of bias, and the exponential shaped OR-TL (OR-TL/EXP) relation resulted in the most when the various relations were examined across methods.

Sigmoid-shaped OR-TL relation

Of the four functions fitted to the OR-TL/SIG relation (Table 3), the Weibull cumulative function resulted in the highest coefficient of determination (r^2=0.914); however the coefficient of determination of the quadratic fit was very similar (r^2=0.913).

Table 3

Summary of the combination of OR-TL and back-calculation models that resulted in the best lack-of-fit (lowest sum of squares [SS]) for each of the four shapes of OR-TL examined

	Best lack-of-fit result	
OR-TL shape	OR-TL model	Back-calculation model
Sigmoid		
All annuli	linear regression, model I	$\log_e(L_n) = \log_e(L_c) + b(\log_e(R_n) - \log_e(R_c))$
Last annulus only	none	$L_n = (R_n / R_c) L_c$
Linear		
All annuli	linear regression, model II	$L_n = a + (R_n / R_c)(L_c - a)$
Last annulus only	linear regression, model II	$L_n = a + (R_n / R_c)(L_c - a)$
Exponential		
All annuli	quadratic equation	$L_n = c + (dR_n) + (eR_n^2) + (fR_n^3)$
Last annulus only	quadratic equation	$L_n = c + (dR_n) + (eR_n^2) + (fR_n^3)$
Asymptotic		
All annuli	Weibull cumulative function	$L_n = (K(L_c / L_p))(1 - \exp(-(R_n / \alpha)^\beta))$
Last annulus only	Weibull cumulative function	$L_n = (K(L_c / L_p))(1 - \exp(-(R_n / \alpha)^\beta))$

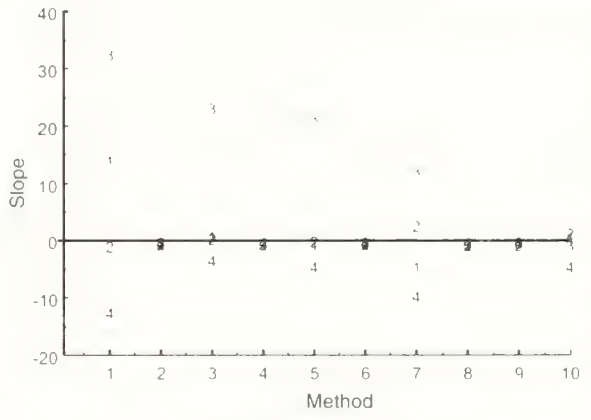

Figure 3

Scatterplot of the slopes of the regression of back-calculated length at age 2 versus age at capture for the ten back-calculation methods that used all annuli. The numbers plotted indicate the shape of the OR-TL relation examined (1=OR-TL/SIG [sigmoid], 2=OR-TL/LIN [linear], 3=OR-TL/EXP [exponential], 4=OR-TL/ASYM [asymptotic]).

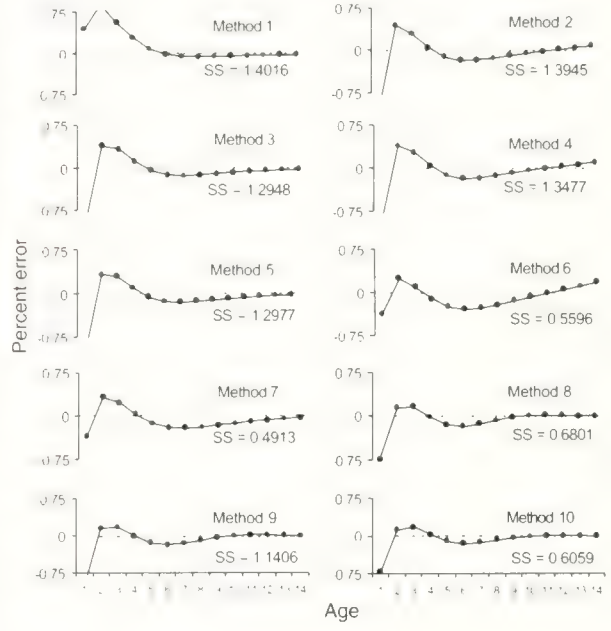

Figure 4

Error in mean length at age estimates using all annuli and the ten back-calculation methods outlined in Table 1 for the sigmoid-shaped OR-TL relation. SS = sum of squares.

The sigmoid shape of the OR-TL relation was evident in the shape of the percent error plots for methods 1 through 10 (Fig. 4). When the OR-TL relation was sigmoid-shaped and all annuli were used, the least error resulted from employing a ordinary least-squares regression coupled with the log-transformed Fraser-Lee back-calculation equation (method 7, SS=0.4913). The greatest error appeared when using the direct proportion equation (Fig. 4, method 1, SS=1.4016). Using the y-intercept of the OR-TL relation in the back-calculation equation (methods 3/13 and 5/14 in Table 1) had little effect on the total sum of squares when comparing method 2 with method 3; in addition, correcting for different limits of the Weibull function in methods 8 versus 10 had little effect. However, the log transformation of methods 6 and 7 reduced the sum of squares considerably.

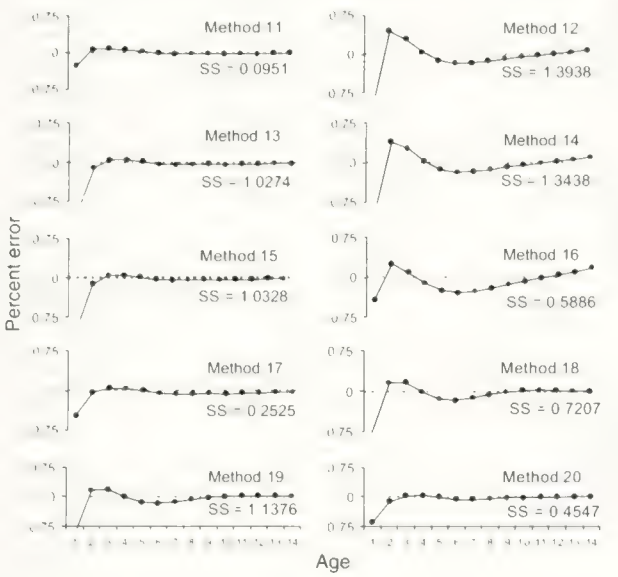

Figure 5

Error in mean length at age estimates using the last annulus only and the ten back-calculation methods outlined in Table 1 for the sigmoid-shaped OR-TL relation. SS = sum of squares.

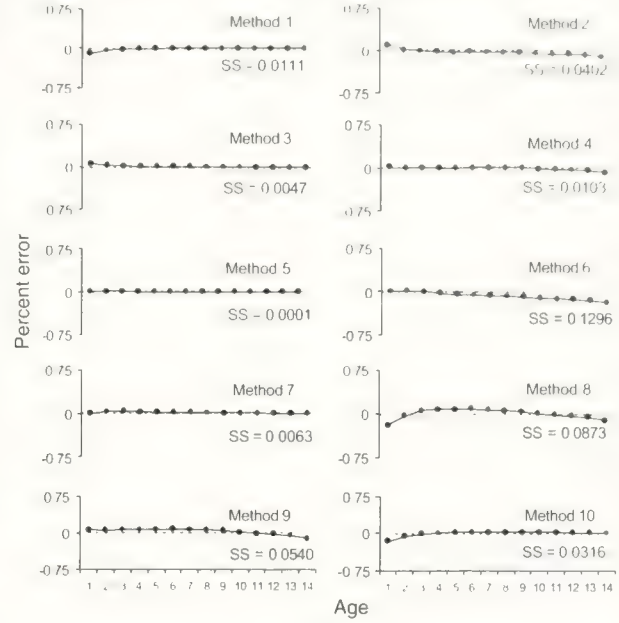

Figure 6

Error in mean length at age estimates using all annuli and the ten back-calculation methods outlined in Table 1 for the linear-shaped OR-TL relation. SS = sum of squares.

The sigmoid shape of the OR-TL relation was not as evident in the shape of the percent error plots for methods 11 through 20 (Fig. 5). When only the last annulus was used, the least error resulted from employing a direct proportionality back-calculation equation (Fig. 5, method 11, SS=0.0951), and the greatest error from using direct substitution into the OLS regression equation (Fig. 5, method 12, SS=1.3938). When only the last annulus was used with comparable back-calculation equations, as in methods 12 versus 13 and 18 versus 20, both the sum of squares and bias were reduced considerably.

Linear-shaped OR-TL relation

Of the four functions fitted to OR-TL/LIN, the ordinary least squares and functional linear regressions resulted in the highest coefficient of determination value (r^2=0.916). The curvature of the Weibull and quadratic fits showed that the relation deviated slightly from a straight line.

There was a high degree of similarity between the percent error plots for all twenty methods (Figs. 6 and 7), suggesting that the estimation of length-at-age is not as sensitive to the method of back-calculation when the OR-TL relation is linear as when it is curved. When the OR-TL relation was linear, the least error resulted from employing a functional regression coupled with the Fraser-Lee back-calculation equation when all annuli were used (Fig. 6, method 5, SS=0.0001) and when only the last annulus was used (Fig. 7, method 15, SS=0.0013). The greatest error resulted from direct substitution into the OLS regression following a natural log transformation of all parameters, both when all annuli were used (Fig. 6, method 6, SS=0.1296) and when only the last annulus (Fig. 7, method 16, SS=0.1245).

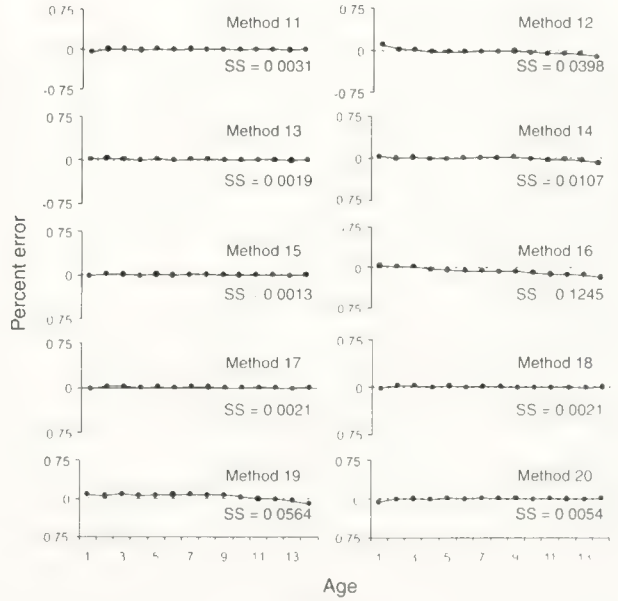

Figure 7

Error in mean length at age estimates using the last annulus only and the ten back-calculation methods outlined in Table 1 for the linear-shaped OR-TL relation. SS = sum of squares.

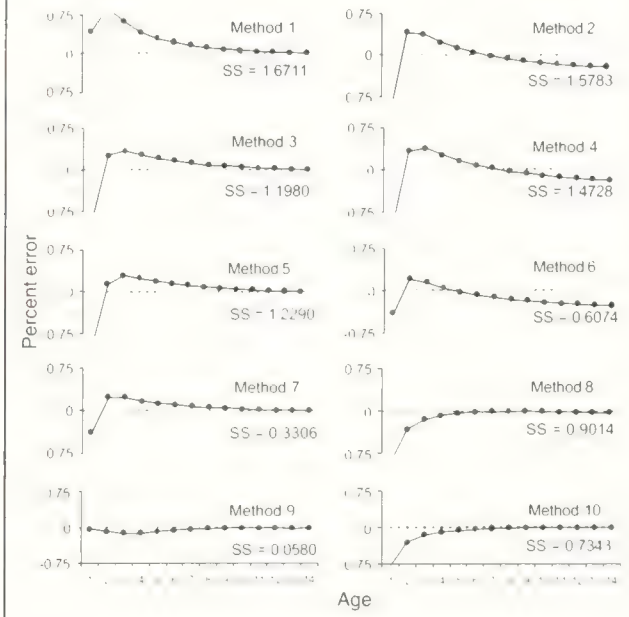

Figure 8

Error in mean length at age estimates using all annuli and the ten back-calculation methods outlined in Table 1 for the exponentially shaped OR-TL relation. SS = sum of squares.

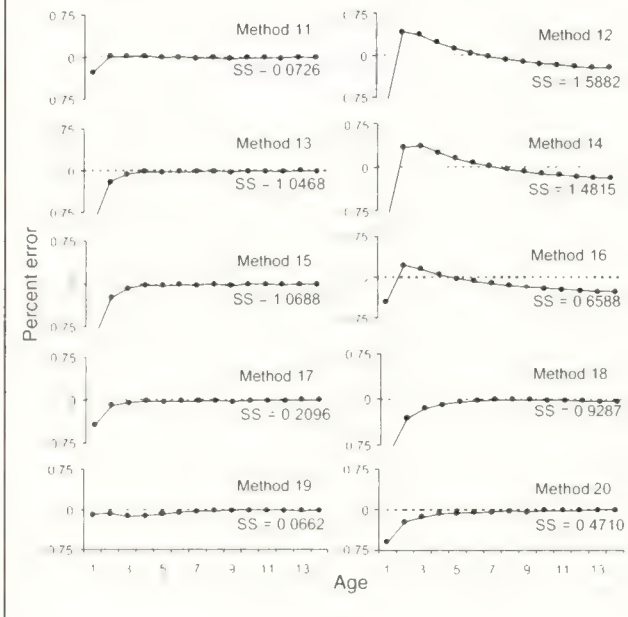

Figure 9

Error in mean length at age estimates using the last annulus only and the ten back-calculation methods outlined in Table 1 for the exponentially shaped OR-TL relation. SS = sum of squares.

Exponentially shaped OR-TL relation

Of the four functions fitted to OR-TL/EXP, the quadratic function resulted in the highest coefficient of determination (r^2=0.883); however the coefficient of determination of the Weibull function fit was nearly as high (r^2=0.878). The percent errors, when using all annuli and linear regression, followed a pattern similar to the residuals of the OR-TL relation (Fig. 8). This trend was also evident, although not as strong, when only the last annulus was used (Fig. 9). Using the quadratic function rather than the linear regression to fit the OR-TL relation did the most at removing this bias (Fig. 8 method 9, and Fig. 9 method 19).

When the OR-TL relation was exponentially shaped and all annuli were used, the least error resulted from direct substitution into the fitted quadratic equation (Fig. 8, method 9, SS=0.0580), and the greatest error from using the direct proportionality equation (Fig. 8, method 1, SS=1.6711). When only the last annulus was used, the least error resulted from direct substitution into the fitted quadratic equation (Fig. 9, method 19, SS=0.0662), and the greatest error from using direct substitution into the OLS regression equation (Fig. 9, method 12, SS=1.5882).

Asymptotically shaped OR-TL relation

Of the four functions fitted to OR-TL/ASYM, the quadratic equation resulted in the highest coefficient of determination (r^2=0.963); however the coefficient of determination of the Weibull function fit was nearly as high (r^2=0.958). As with the exponentially shaped OR-TL relation, when linear regression was used to model the OR-TL relation, the percent error by age followed the trend of residuals for the residuals for the regression (Fig. 10). Using the last annulus only resulted in generally lower sums-of-squares, especially when the y-intercept was corrected for log transformation of the OR-TL relation used (Fig. 11).

When the OR-TL relation was asymptotically shaped and all annuli were used, the least error resulted from using the individually corrected Weibull cumulative distribution function (Fig. 10, method 10, SS=0.7388), and the greatest error from using direct substitution in to the OLS regression equation (Fig. 10, method 2, SS=1.9319). When only the last annulus was used, the least error again resulted from using the individually corrected Weibull cumulative distribution function (Fig. 11, method 20, SS=0.0516), and the greatest error from using direct substitution in to the OLS regression equation (Fig. 11, method 12, SS=1.9261).

Discussion

The most accurate estimates of length-at-age resulted from the best model fits of the OR-TL relation. Even though sampling was random, poorly fitted OR-TL regressions resulted in back-calculation tables with obvious "Lee's phenomenon" effects. Ricker (1969) pointed out that the use of an incorrect otolith radius-total length relationship can result in this effect. Smale and Taylor (1987) also

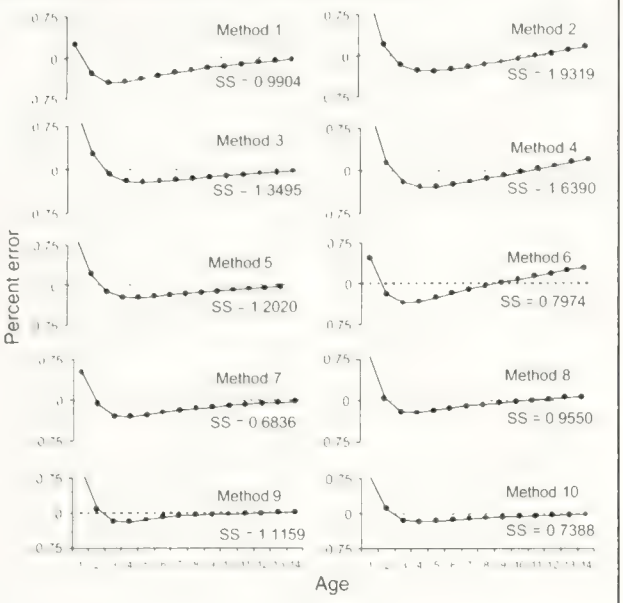

Figure 10

Error in mean length at age estimates using all annuli and the ten back-calculation methods outlined in Table 1 for the asymptotically shaped OR-TL relation. SS = sum of squares.

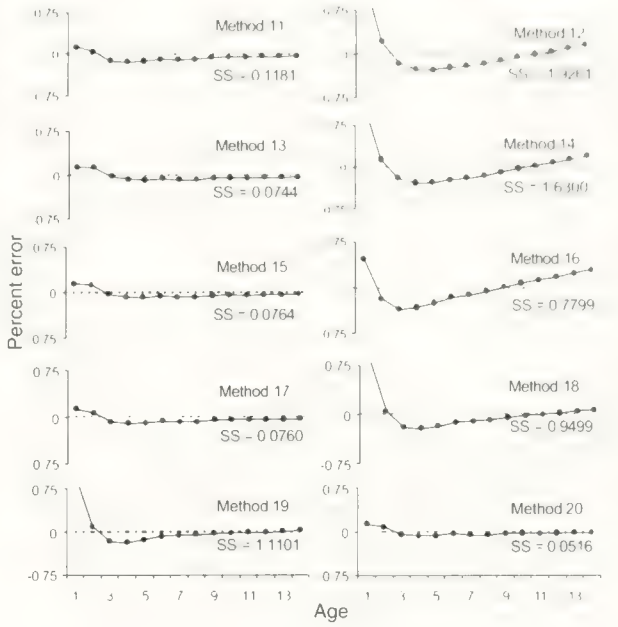

Figure 11

Error in mean length at age estimates by using the last annulus only and the ten back-calculation methods outlined in Table 1 for the asymptotically shaped OR-TL relation. SS = sum of squares.

showed that using the improper back-calculation method can result in a false "Lee's phenomenon" effect. Using only the last annulus reduced this effect with some back-calculation methods in this study, but not all of them. In general, the accuracy of the estimated length-at-age was directly related to how well the particular model fitted the OR-TLrelation, suggesting that the OR-TL model is just as, if not more, important as selecting the appropriate back-calculation model.

Based on the importance of the fit of the OR-TL model, it follows that the methods used to sample the catch are of equal importance. Nonrandom samples of the catch, or length-based regulations that cause the catch to misrepresent the population, will affect the OR-TL regression. For instance, a minimum legal size will artificially truncate the OR-TL relation in samples of the catch and selectively sample faster-growing small fish. This could eliminate the youngest ages from the regression and could necessitate extrapolation of the regression beyond the range of the data. Furthermore, a truncation of the OR-TL regression would positively bias the y-intercept and lead to an overestimation of length-at-age, especially for the younger ages.

It has been pointed out that univariate statistical models, which assume independence of observations, are generally inappropriate for analysis of otolith increment data (Chambers and Miller, 1995). These authors have suggested that because otolith data constitute multiple measures, perhaps examination of the covariance is more appropriate than the comparison of individual means. In this study, however, I did not seek to emphasize the existence of (or lack of) a statistical difference between the true and estimated means sizes. Given the large sample sizes made available through simulation, conclusions of significant differences resulting from any statistical tests can be misleading. More useful, I believe, is the shape, direction, and magnitude of the biases that emerged from each back-calculation method. Consequently, I chose to emphasize the percent error between the true and estimated mean size-at-age. Using percent error allows more freedom of interpretation and is not subject to the problems associated with excessively large degrees of freedom of simulated data sets.

The individually corrected Weibull cumulative distribution function presented here proved to be very flexible and capable of accounting for the individual otolith radius-total length trajectories. This function is very similar to the linear y-intercept corrected back-calculation equation of Fraser-Lee but can accommodate a wide varieties of curvatures. The Weibull equation I reported (Eq. 13) has an origin at x and y of 0; however, a y-intercept term can easily be added to accommodate an OR-TL relation with a nonzero intercept.

Much of the cohort's diversity in biological attributes was lost within the first few months of the life because of mortalities. By the time the cohort had completed one year of growth, the diversity in biological attributes of the individuals that would ultimately represent the cohort were established. Based on the observations of Secor and Houde (1995), the establishment of the biological attributes of a

cohort occurring after one year is a realistic representation of what occurs in the early life history of striped bass. Although the number of fish that a cell represented could be less than one, this number was used as a relative weighting to all other cells; thus, proportionally, the value was valid. Consequently, the actual starting number of fish of the cohort was irrelevant for this study but could be used to calibrate the model to a particular population of interest.

I was able to simulate a number of dissimilarly shaped OR-TL relationships by modifying the parameter used to convert brain weight to otolith weight from a constant to a function. However, trial runs showed that when this parameter was held constant, the resulting OR-TL relation was not linear. I later determined that because both soma and otolith growth were modeled as functions of weight and because the exponent of the weight-length equation (0.31) did not exactly equal the exponent of the equation that calculates the radius of a sphere (0.333), two rates must at some point diverge from linearity. For the purposes of this study, it was not necessary that the equations precisely depict the actual bioenergetics processes, only that true length of fish at annulus formation be known with certainty.

This study yields several conclusions important to studies of growth estimates from otolith back-calculations. The best back-calculation technique was directly related to how well the OR-TL model fitted. The percent error of any given method was rarely consistent across ages, although estimates of older ages were more accurate than those of younger ones. Younger ages were generally best estimated by using direct proportionality on the last annulus only. Thus, it may be necessary to use multiple methods to accurately estimate a growth curve. However, it would be difficult to select which combination of methods would be most accurate without prior knowledge of the true length-at-age.

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Sustainability of elasmobranchs caught as bycatch in a tropical prawn (shrimp) trawl fishery

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Abstract—The bycatch of Australia's northern prawn fishery (NPF) comprises 56 elasmobranch species (16 families). The impact of this fishery on the sustainability of these species has not been addressed. We obtained estimates of catch rates and the within-net survival of elasmobranchs. *Carcharhinus tilstoni, C. dussumieri, Rhynchobatus djiddensis,* and *Himantura toshi* represented 65% of the bycatch. For most species, >50% of individuals in the bycatch were immature, and some species recruited to the fishery at birth. For all species combined, 66% of individuals in the bycatch died in the trawl net.

The relative sustainability of elasmobranchs caught as bycatch was examined by ranking species with respect to their susceptibility to capture and mortality due to prawn trawling and with respect to their capacity to recover once the population was depleted. The species that were least likely to be sustainable were four species of pristids, *Dasyatis brevicaudata,* and *Himantura jenkinsii.* These are bottom-associated batoids that feed on benthic organisms and are highly susceptible to capture in prawn trawls. The recovery capacity of these species was also low according to our criteria. Our results provide a valuable first step towards ensuring the sustainability of elasmobranchs that are caught as bycatch by highlighting species for management and research. The effectiveness of turtle excluder devices (TEDs) in reducing elasmobranch bycatch varied greatly among species but was generally not very effective because most of the captured species were small.

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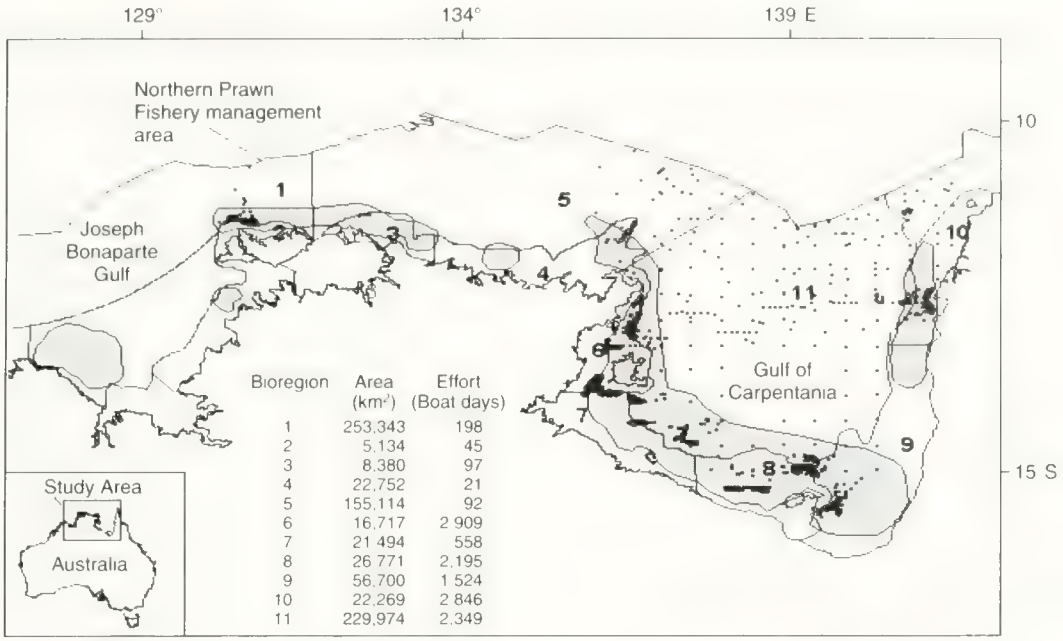
Worldwide, there is increasing concern over the capture of elasmobranchs (sharks and rays) as bycatch. The global landings of elasmobranchs are currently 760,000 metric tons (t) but a similar amount is part of unreported bycatch (Stevens et al., 2000). This bycatch is unmanaged in most fisheries and elasmobranchs are less able to sustain their populations under fishing regimes designed to sustain the target teleosts or invertebrates (Heuter, 1998). Some species have declined significantly because they are captured as bycatch, e.g. the common (*Dipturus batis*) and barndoor (*D. laevis*) skates (Brander, 1981; Casey and Myers, 1998). Despite these prevailing fishery practices, there have been few evaluations of the ability of elasmobranch species to sustain population levels (Walker and Hislop, 1998).

In general, an evaluation of the sustainability of any bycatch species is hampered by a lack of information. This is particularly so for elasmobranchs. Elasmobranch bycatch is often not recorded (Bonfil, 1994), or when it is recorded, the species composition is unknown. There is also limited biological information on most bycatch species, such as age at maturity, growth rate, and fecundity. This lack of information hampers the use of conventional stock assessment methods to determine the population status of these species.

Australia has a highly diverse elasmobranch fauna; almost half of the species are endemic (Last and Stevens, 1994). In northern Australian waters, elasmobranchs are impacted by a range of fisheries. Gillnet, longline, and dropline fisheries target shark species. Sharks, rays, and sawfish are also caught as bycatch in dropline and gillnet fisheries that target teleosts and in trawl fisheries that target teleosts or prawns. The current levels of elasmobranch bycatch are unknown for most of these fisheries. However, we know that the retained elasmobranch bycatch has increased because of the rising value of elasmobranch products, such as fins.

The largest fishery in northern Australia is the northern prawn fishery (NPF), which covers an area over 1,000,000 km^2 of ocean (Fig. 1) (McLoughlin et al., 1997). In the NPF, elasmobranchs contribute about 4% of the total bycatch weight (Stobutzki et al., 2001b). Prior to 2001, NPF trawlers were allowed to retain shark products but were restricted with respect to the amount on board at any one time. Management required fishermen to record retained bycatch in trawler logbooks, but the records were not validated. In 1999, 4177 kg of fillet, trunk, and whole shark and 1531 fins were recorded (Sharp et al.[1]). The compulsory use of turtle excluder devices (TEDs) in NPF trawls, beginning with the year 2000, have excluded some elasmobranchs from the bycatch (Brewer et al., 1998). However species-specific exclusion has not been examined.

[1] Sharp, A., J. Malcolm, and J. Bishop. 2000. Northern prawn fishery and Kimberley prawn fishery data summary 1999. Final report to Australian Fisheries Management Authority, Canberra, Australia. AFMA, PO Box 7051, Canberra BC ACT 2610, Australia.



Bioregion	Area (km^2)	Effort (Boat days)
1	253,343	198
2	5,134	45
3	8,380	97
4	22,752	21
5	155,114	92
6	16,717	2 909
7	21 494	558
8	26 771	2,195
9	56,700	1 524
10	22,269	2 846
11	229,974	2,349

Figure 1

The management area of the northern prawn fishery (NPF) and the bioregions defined through the interim marine and coastal rationalization (IMCR) process (Thackway and Cresswell, 1998). The shaded area represents the regions fished by commercial prawn trawlers. The dots mark the positions of the trawls that were sampled to estimate the removal rates and total biomass of bycatch species (Table 1). The numbers refer to the bioregions (1=Oceanic Shoals, 2=Tiwi, 3=Cobourg, 4=Arnhem Wessel, 5=Arafura, 6=Groote, 7=Pellew, 8=Wellesley, 9=Karumba-Nassau, 10=West Cape York, 11=Carpentaria).

This study is one of several (Milton, 2001; Stobutzki et al., 2001a) that broadly examine the sustainability of bycatch species groups in the NPF. The aim of this study was to assess the relative sustainability of elasmobranch species taken as bycatch in the NPF. We use a broadbrush method developed by Stobutzki et al (2001a) to encompass the high diversity of and limited amount of information. This semiquantitative technique assesses the sustainability of species according to two overriding characteristics: 1) their susceptibility to capture and mortality due to trawling; and 2) the ability of a population to recover after depletion. Traditional population assessment methods have attempted to measure or model these factors. The broadbrush method uses biological and ecological criteria to rank species with respect to these two characteristics, maximizing the use of the limited information available. The method identifies species that are least likely to be sustainable in the bycatch, so that these can be the focus of further research and management.

Methods

Species present in the NPF and those captured as bycatch

A list of the elasmobranchs species recorded in the area of the NPF was compiled from Last and Stevens (1994). A list of species taken as NPF bycatch has been collated from two sources: 1) fishery research surveys undertaken within the NPF fishing grounds (Crocos and Coman, 1997; Stobutzki et al., 2001b; Blaber et al.[2]; Crocos et al.[3]); and 2) records of elasmobranch bycatch by observers on commercial vessels (these observers were either scientific staff or trained crew-members) (Stobutzki, 2001b; Pender et al.[4]; Stobutzki et al.[5]).

[2] Blaber, S., D. Brewer, C. Burridge, M. Farmer, D. Milton, J. Salini, Y-G. Wang, T. Wassenberg, C. Buxton, I. Cartwright, S. Eayrs, N. Rawlinson, R. Buckworth, N. Gill, J. MacCartie, R. Mounsey, and D. Ramm. 1997. Effects of trawl design on bycatch and benthos in prawn and finfish fisheries. Final report to Fisheries Research and Development Corporation (FRDC), Project 93/179, 190 p. FRDC, PO Box 222, Deakin West ACT 2600, Australia.

[3] Crocos, P. J., D. M. Smith, and G. Marsden. 1997. Factors affecting the reproductive performance of captive and wild broodstock prawns. Final report to the Fisheries Research and Development Corporation (FRDC), Project 92/51, 87 p. FRDC, PO Box 222, Deakin West ACT 2600, Australia.

[4] Pender, P. J., R. S. Willing, and D. C. Ramm. 1992. Northern prawn fishery bycatch study: distribution, abundance, size and use of bycatch from the mixed species fishery. Northern Territory Department of Primary Industry and Fisheries (NT DPIF), fishery report 26, 97 p. NT DPIF, GPO Box 3000, Darwin NT 0801, Australia.

[5] See next page for footnote 5.

Estimates of current bycatch rates and size frequency of species

Current bycatch rates were obtained from research and observer surveys. The research surveys and gear are described in detail in Stobutzki et al. (2001b) and Stobutzki et al.[5] Briefly, the research surveys sampled the nine major NPF fishing regions (1997 and 1998) to describe the bycatch. A scientific observer conducted three trips (of one-month duration) on commercial vessels in the NPF during 1996–97. A crew member of the commercial fleet was trained in elasmobranch identification and recorded the elasmobranch catch on commercial vessels during 1997. All elasmobranchs caught were identified, most to species, and their total number and weight were recorded. Where possible, each individual's sex, weight, and length were recorded. Total length (TL) was recorded for sharks, rhynchobatids, and pristids, and disc width (DW) was recorded for the remaining rays. Trawls during the research survey were of 0.5-h duration and a single trawl net was used. The observer data were collected from commercial trawls, 3–4 h in duration and where two nets were towed.

The overall catch rate for each species was calculated from the three sources. Catch rates were corrected for duration of the trawl and the length of the headrope. The catch rates of species in each trawl were converted into catch per swept area of the trawl as the numbers of individuals per square kilometer swept (no./km^2). We used the trawl speed recorded during the trawls and assumed that the prawn trawls had a spread of 0.66 of the headrope length (Bishop and Sterling, 1999). Individuals of the species *Carcharhinus tilstoni* and *C. limbatus* are difficult to distinguish. Genetic studies in this region have indicated that *C. limbatus* is very rare (Lavery and Shaklee, 1991); therefore all specimens were recorded as *C. tilstoni*.

Size at first maturity and fecundity

Because there is limited biological information on dasyatidids and gymnurids (Last and Stevens, 1994), we retained specimens from the scientific surveys to obtain preliminary estimates of size at maturity and fecundity. For females, gonad weight, diameter of the largest ovum in the ovary, and their fecundity status (whether they were pregnant of not, and whether there were *in utero* embryos present) were recorded. For pregnant individuals, the number of embryos was recorded. For males, we recorded gonad weight, clasper length, and the calcification state of the clasper (uncalcified, partially calcified, or totally calcified). Size at sexual maturity for females was estimated as the length of the smallest pregnant individual; for males it was determined from clasper size and calcification (Bass et al., 1973).

Within-net survival

Currently there is no information on the survival rate of elasmobranchs caught as bycatch in prawn trawlers. The October 1998 research survey and crew-member observer (Table 1) recorded whether individuals were dead or alive when landed on the deck. This record provided an estimate of the within-net mortality, which was no doubt lower than the total mortality because some individuals recorded as alive would subsequently die as a result of capture. Logistic regressions (PROC LOGISTIC, SAS 1997) were used to determine whether there was a relationship between the likelihood of survival and the length or sex of an individual. The species were analyzed in two groups: sharks (species where TL was recorded) and rays (species where DW was recorded).

Assessment of the sustainability of elasmobranch species

The assessment was based on the method developed by Stobutzki et al. (2001a) which was designed to accommodate a high diversity of and a limited amount of information. The sustainability of the species was assumed to be dependent on two overriding features: 1) the susceptibility of the species to capture and mortality caused by trawling and 2) the capacity of the population to recover after depletion. Biological and ecological information was collated from the literature (Compagno, 1984a; 1984b; Last and Stevens, 1994; Froese and Pauly[6]). This information was used to rank the species along two axes describing the overriding features:

Axis 1: The susceptibility of a species to capture and mortality due to a prawn trawl (susceptibility),
Axis 2: The capacity of a species to recover once the population is depleted (recovery).

Each feature (or axis) was derived from several criteria (listed below) that summarized aspects of the biology of the species (six criteria for axis 1 and five criteria for axis 2). Each species was given a ranking from 1 to 3 for each criterion (the definitions of the ranks for the criteria are provided in Table 2). A rank of 1 suggested that the species was highly susceptible to capture or had little capacity to recover; a rank of 3 suggested that the species had a low susceptibility to capture or a high capacity to recover. Depending on the criterion, these ranks were based on categorical or continuous data (Table 2). Where continuous data were used, because no information was available to assign divisions between the ranks, the range of the data was divided into thirds to create the categories.

[5] Stobutzki, I., S. Blaber, D. Brewer, G. Fry, D. Heales, P. Jones, M. Miller, D. Milton, J. Salini, T. Van der Velde, Y-G. Wang, T. Wassenberg, M. Dredge, A. Courtney, K. Chilcott, and S. Eayrs. 2000. Ecological sustainability of bycatch and biodiversity in prawn trawl fisheries. Final report to the Fisheries Research and Development Corporation (FRDC), Project 96/257, 512 p. FRDC, PO Box 222, Deakin West ACT 2600, Australia.

[6] Froese, R., and D. Pauly, eds. 1999. Fishbase 99. URL htpp://www.fishbase.org. [Date accessed: November 1999.]

Table 1

The surveys that contributed to the estimate of the removal rate (*), total biomass, and within-net survival for elasmobranch species in the Northern Prawn Fishery, Australia. # indicates the surveys whose data contributed to the list of bycatch species.

Year	Month	Type	Gear	No. of trawls	No of nets used	Reference
1998*#	Sep–Oct	research survey	Florida flyer	366	1	Stobutzki et al.[5]
1997*#	Oct	research survey	Florida flyer	424	1	Stobutzki et al. (2001b)
1997*#	Sep–Oct	scientific observer	Florida flyer	60	2	Stobutzki et al. (2001b)
1997*#	Aug–Oct	crew member observer	Florida flyer	141	2	Stobutzki et al.[5]
1997*#	May–Jun	scientific observer	Florida flyer	76	2	Stobutzki et al. (2001b)
1997*#	Feb–Mar	research survey	Florida flyer, Engels	248	1	Stobutzki et al. (2001b)
1996*#	Sep	scientific observer	Florida flyer	83	2	Stobutzki et al. (2001b)
1995#	Jun	research survey	Florida flyer	38	1	Blaber et al.[2]
1995#	Oct–Nov	research survey	Florida flyer	39	1	Blaber et al.[2]
1995#	Feb–Mar	research survey	Florida Flyer	39	1	Blaber et al.[2]
1994#	Nov	research survey	Florida flyer	7	2	Crocos and Coman (1997); Crocos et al.[3]
1994#	Jul	research survey	Florida flyer	7	2	Crocos and Coman (1997); Crocos et al.[3]
1994#	Ma	research survey	Florida flyer	4	2	Crocos and Coman (1997); Crocos et al.[3]
1994#	Mar	research survey	Florida flyer	5	2	Crocos and Coman 1997; Crocos et al.[3]
1993#	Nov	research survey	Florida flyer	81	1	Crocos and Coman 1997; Crocos et al.[3]
1993#	Oct	research survey	Florida Flyer	5	2	Blaber et al.[2]
1993#	Aug	research survey	Florida Flyer	9	2	Crocos and Coman (1997; Crocos et al.[3]
1993	Jan–Feb	research survey	Engels, Frank and Bryce	71	1	Milton et al. (1995)
1991	Nov	research survey	Frank and Bryce	62	1	Milton et al. (1995)
1990	Nov–Dec	research survey	Frank and Bryce	128	1	Blaber et al. (1994); Milton et al. (1995)

Where species-specific information was not available, a species was given the same rank as other species within its family for the criteria water column position, diet, and day and night catchability. For the other criteria, where it was not necessarily logical that family members would be similar, or where family information was not available, a rank of 1 was assigned as a precautionary approach.

Axis 1: Susceptibility of a species to capture and mortality induced by the prawn trawl

There were six criteria (water column position, survival, range, day and night catchability, diet, and depth range) on axis 1.

Water column position Because prawn trawls fish close to the sea floor, demersal species are more likely to be captured than pelagic species.

Survival This estimate was based on the survival-in-the-net data outlined previously. The possible survival range of 0–100% was divided into thirds for the divisions between the ranks.

Range This criterion reflects the geographic spread of a species within the NPF and was determined from the research, scientific, and crew-member observer surveys undertaken by Stobutzki et al.[5] and Stobutzki et al. (2001b). Commercial fishing is highly aggregated within the managed area of the fishery. The nine regions of highest effort were surveyed in 1997 (Table 1) and the presence or absence of each species was recorded in each region. We assumed that species with a restricted range could be impacted more heavily by trawling than those with a broader range.

Day and night catchability The tiger prawn fishery is predominantly a nighttime fishery (McLoughlin et al., 1997). Species with a higher catchability at night are more susceptible to capture as bycatch. The relative catch rate of species during night and daytime trawling was compared during research surveys in October 1997 (Table 1).

Diet This criterion reflects whether the diet of the species may attract them to trawl grounds and whether they feed within the area of the water column swept by a prawn trawl. Species that feed on commercial prawns may be attracted to the commercial fishing grounds, increasing their susceptibility to capture. Species that feed on demersal organisms are assumed to be more susceptible to prawn trawls than species that feed higher in the water column.

Depth range Commercial trawls in the NPF are made mainly between 15 m and 40 m (Somers, 1994). An overlap between the depth range of trawling and the preferred

Table 2

The criteria used to assess 1) the relative susceptibility of bycatch species to capture and mortality due to prawn trawls and 2) their recovery capacity after depletion due to trawling. These combine to provide the ranks for the axes in Figure 2. For each criterion the definition of the three ranks is given, as well as the weighting score and the percentage of species for which species-specific information was used to rank them.

Criteria	Weight	Species-specific information (%)	Rank 1	Rank 2	Rank 3
Susceptibility					
Water column position	3	100	Demersal or benthic	Not applicable	Benthopelagic or pelagic
Survival	3	18	Probability of survival <33%	Probability of survival between 33% and 66%, inclusive	Probability of survival >66%
Range	2	71	Species range ≤3 fishery regions	3 fishery regions < species range ≤6 fishery regions	Species range >6 fishery regions
Day and night catchability	2	32	Higher catch rate at night	No difference between night and day	Higher catch rate at day
Diet	2	55	Known to, or capable of, feeding on commercial prawns or benthic organisms	Not applicable	Feed on pelagic organisms
Depth range	1	100	Less than 60 m	Not applicable	Deeper than 60 m
Recovery					
Probability of breeding	3	42	Probability of breeding before capture <50%	Probability of breeding before capture not significantly different from 50%	Probability of breeding before capture >50%
Maximum size	3	100	Maximum disc width >1755 mm Maximum total length >4781 mm	853 mm < maximum disc width ≤1755 mm 1861 mm < maximum total length ≤4781 mm	Maximum disc width ≤853 mm Maximum total length ≤1861 mm
Removal rate	3	79	Removal rate >66%	33% < removal rate ≤66%	33% ≤ removal rate
Annual fecundity	1	52	Annual fecundity ≤5 young per year	5 young per year < annual fecundity ≤19 young per year	Annual fecundity >19 young per year
Mortality index	1	64	mortality index >3.47	0.92 < mortality index ≤3.47	mortality index ≤0.92

depth range of species will influence their susceptibility to capture: a higher proportion of a species' population is likely to be taken if there is an overlap. Species with a broader depth range may have a spatial refuge from trawling, making them less susceptible. The depth range of species was determined from previous research surveys in the NPF and from the literature.

Axis 2: The capacity of a species to recover once the population is depleted

There were five criteria (probability of breeding, maximum size, removal rate, annual fecundity, mortality index) on this axis.

Probability of breeding We assumed that a species is likely to have a greater capacity to recover from a decrease in population due to trawling if most individuals are captured after they have bred. The probability that an individual of a species had bred before capture was determined from the mean length at capture in relation to the species' recorded size at maturity. The mean length at capture of a species was recorded in the research and observer surveys 1996–98 (Table 1). Size at maturity was determined from the available literature and from our estimates outlined previously.

A *t*-test (Sokal and Rohlf, 1996) was used to determine whether the mean length at capture was significantly different from the size at maturity for each species.

Table 3

The elasmobranch species that are known to occur in the region of the northern prawn fishery (NPF), Australia, and of these species, those that have been recorded in NPF bycatch (Table 1). The labels in parentheses refer to the species abbreviations in Figure 2.

	Recorded in bycatch		
Family	Yes		No
Carcharhinidae	*Carcharhinus albimarginatus*	(Cal)	*Carcharhinus amblyrhynchoides*
	Carcharhinus amboinensis	(Cam)	*Carcharhinus amblyrhynchos*
	Carcharhinus brevipinna	(Cb)	*Carcharhinus cautus*
	Carcharhinus dussumieri	(Cd)	*Carcharhinus obscurus*
	Carcharhinus fitztroyensis	(Cf)	*Carcharhinus plumbeus*
	Carcharhinus leucas	(Cle)	*Carcharias taurus*
	Carcharhinus limbatus	(Cli)	*Carcharinus falciformis*
	Carcharhinus macloti	(Cm)	*Carcharinus melanopterus*
	Carcharhinus sorrah	(Cs)	*Loxodon macrorhinus*
	Carcharhinus tilstoni	(Ct)	*Rhizoprionodon oligolinx*
	Galeocerdo cuvier	(Gc)	*Triaenodon obesus*
	Negaprion acutidens	(Na)	
	Prionace glauca	(Pg)	
	Rhizoprionodon acutus	(Rac)	
	Rhizoprionodon taylori	(Rta)	
Dasyatidae	*Amphotistius annotata*	(Aa)	*Dasyatis fluviorum*
	Dasyatis brevicaudatus	(Db)	*Taeniura lymma*
	Dasyatis leylandi	(Dl)	
	Dasyatis kuhlii	(Dk)	
	Dasyatis sp. A	(Dsa)	
	Dasyatis thetidis	(Dt)	
	Himantura fai	(Hf)	
	Himantura granulata	(Hg)	
	Himantura jenkinsii	(Hj)	
	Himantura sp. A	(Hsa)	
	Himantura toshi	(Ht)	
	Himantura uarnak	(Hua)	
	Himantura undulata	(Hun)	

continued

Maximum size The maximum size of a species was used as an indicator of the species' relative recovery rate. In general, larger species tend to live longer and their populations recover more slowly (Roberts and Hawkins, 1999). Size appears to be a good predictor of vulnerability for marine fishes (Jennings et al., 1999), and in particular skates (Walker and Hislop, 1998; Dulvy et al., 2000). Estimates of maximum size came from the literature. Species were grouped according to whether DW or TL was measured. The range of the maximum sizes of species was calculated and divided into thirds for the divisions between the ranks.

Removal rate We assumed that species with a higher proportion of their biomass removed as bycatch would have a lower capacity to recover. The estimate of removal rate was based on the catch rates from research surveys and scientific observer collections undertaken between 1996 and 1998 (Table 1). We assumed that these catch rates were representative of the overall catch rates in the commercial fishery.

The catch rates of bycatch species vary spatially within the NPF (Stobutzki et al., 2001b). Therefore, the fishery was stratified before we estimated the mean catch rate, using the bioregions identified in the Interim Marine and Coastal Regionalization for Australia (IMCRA) process (Thackway and Cresswell, 1998) (Fig. 1). A mean catch rate for each species was calculated for each bioregion where commercial tiger prawn trawling occurs.

The biomass (in numbers of individuals per year) of bycatch removed by the commercial fishery was estimated by multiplying the mean catch rate calculated above by the 1997 commercial tiger prawn fishery effort in each bioregion (Table 3). Commercial fishing effort is recorded in log books in boat days (held by the Australian Fisheries Management Authority). One boat day was assumed to be the

Table 3 (continued)

Family	Recorded in bycatch: Yes		Recorded in bycatch: No
Dasyatidae (continued)	*Pastinachus sephen*	(Ps)	
	Taeniura meyeni	(Tm)	
	Urogymnus asperrimus	(Ua)	
Ginglymostomatidae	*Nebrius ferrugineus*	(Nf)	
Gymnuridae	*Gymnura australis*	(Ga)	
Hemigaleidae	*Hemigaleus microstoma*	(Hm)	*Hemiscyllium ocellatum*
	Hemipristis elongatus	(He)	*Hemiscyllium trispeculare*
Hemiscylliidae	*Chiloscyllium punctatum*	(Cp)	
Mobulidae			*Manta birostris*
			Mobula eregoodootenkee
Myliobatidae	*Aetobatus narinari*	(Ana)	
	Aetomylaeus vespertilio	(Av)	
	Aetomyleus nichofii	(Ani)	
Narcinidae	*Narcine westraliensis*	(Nw)	*Narcine* sp. A
Orectolobidae	*Orectolobus ornatus*	(Oo)	*Eucrossorhinus dasypogon*
			Orectolobus wardi
Pristidae	Anoxypristis cuspidata	(Ac)	
	Pristis clavata	(Pc)	
	Pristis microdon	(Pm)	
	Pristis pectinata	(Pp)	
	Pristis zijsron	(Pz)	
Scyliorhinidae	*Atelomycterus fasciatus*	(Af)	*Atelomycterus macleayi*
	Galeus sp. A	(Gsa)	
Sphyrnidae	*Eusphyra blochii*	(Eb)	
	Sphyrna lewini	(Sl)	
	Sphyrna mokarran	(Sm)	
Squatinidae	*Squatina* sp. A	(Ssa)	
Stegostomatidae	*Stegostoma fasciatum*	(Sf)	
Rhincodontidae			*Rhiniodon typus*
Rhinobatidae	*Rhinobatos typus*	(Rty)	*Aptychotrema* sp. A
Rhynchobatidae	*Rhynchobatus djiddensis*	(Rd)	
	Rhina ancylostoma	(Ran)	

equivalent of 14 hours of trawling with two nets and with 14-fathom (25.48 m) headropes at a speed of 3.2 knots (5.9 km/h) (Bishop and Sterling, 1999).

The estimate of the total amount removed for a species within the whole fishery was calculated by summing the removal estimates for the bioregions. This estimate was then converted to a proportion of the estimated total biomass of the species.

An estimate of the total biomass of each species in the bioregions where tiger prawn trawling occurs was generated from all research and scientific observer surveys conducted in the NPF during the 1990s (Fig. 1, Table 1). The gears used were prawn trawls (Florida flyer nets) and two types of fish trawls (Frank and Bryce trawls and Engel trawls). Both night and daytime trawling were undertaken. Both prawn-trawl and fish-trawl surveys were analyzed in order to cover the management area of the fishery.

The catch rates of species in each trawl were converted to the catch per swept area of the trawl as described previously. The fish trawls were assumed to have a spread of 0.6 of the headrope length (Blaber et al., 1994). A mean catch rate for each gear at each time (day or night) was calculated in each bioregion, resulting in up to six catch rate estimates for a species in a bioregion. The highest of these means was used for each species in that bioregion. This catch rate was then multiplied by the area of the bioregion to give an estimate of total numbers of individuals in the bioregion. Currently there are no robust estimates of the catchability coefficients for the various trawl gears and therefore a catchability coefficient of one was assumed for

all species. Such a high catchability coefficient is unlikely to be valid for most species and results in an underestimate of the total biomass. For the two bioregions where commercial tiger prawn trawlers operate, there was no survey data from which to estimate catch rates (bioregions 4 and 5, Fig. 1). Therefore, the mean catch rate of the other bioregions was used to allow an estimate of catch rate. The total biomass of each species was calculated by summing the estimates for the bioregions. The removal rate would range between 0% and 100%; this range was divided into thirds for the division between the ranks.

Annual fecundity The annual fecundity of species was estimated from data in the literature and the biological samples collected during our study. The annual fecundity of a species was estimated as the average number of pups per female multiplied by the number of times the females bred per year. Where the frequency of breeding was not known, it was assumed to be annual, unless the known gestation period was longer than 12 months. The range of fecundities was calculated and divided into thirds for the divisions between the ranks.

Mortality index The recovery capacity of a population is likely to be related to its fishing mortality rate (Sparre and Venema, 1992). A measure of this rate can be derived from the length-frequency of a species and the von Bertlanffy growth parameters (Sparre and Venema, 1992). However, for most species von Bertalanffy parameters were not available and therefore an index of mortality was calculated as follows:

$$Mortality\ index = (L_{max} - L_{ave})/(L_{ave} - L_{min}), \quad (1)$$

where L_{max} = the maximum length;
L_{ave} = the mean length at capture in the fishery; and
L_{min} = the smallest length caught.

The closer the mean length of captured individuals (L_{ave}) to the maximum length (L_{max}) the lower the mortality the population is subject to. As mortality due to fishing increases, the mean length of species in a population approaches the minimum length (L_{min}). For our analysis, we assumed constant catchability and mortality across the whole length range caught. The L_{ave} and L_{min} were calculated from length data collected during our study.

The range of mortality estimates was calculated and divided into thirds for the divisions between the ranks.

Analysis of criteria

Partial correlations (Sokal and Rohlf, 1996) were used to determine whether there was any redundancy in the criteria. Strong correlations would suggest that two or more criteria explained the same factors, which would lead to overemphasis of their effect. One of the correlated criteria was, therefore, removed.

The total susceptibility, or removal ranking, of a species was determined by the following equation:

$$S_i = \frac{\sum_{j=1}^{n} w_j R_i}{\sum_{j=1}^{n} w_j}, \quad (2)$$

where S_i = the total susceptibility or recovery ranks for species i;
w_j = the weighting for criterion j;
R_i = the rank of species i for criterion j; and
n = the number of criteria on each axes.

The criteria were weighted to reflect the relative importance of each criterion in determining the overall characteristic and the robustness and quality of the data (Table 2), the latter in terms of the amount of species-specific information and the scale of the information available. The criteria that were seen as major determinants of susceptibility or recovery and for which there were more robust data were weighted highest. This weighting was done in collaboration with the NPF Fishery Assessment Group.

The total susceptibility and recovery ranks for the species were graphed to determine the relative sustainability of the species caught as bycatch by prawn trawlers. The species least likely to be sustainable would be identified as the species with the lowest ranks on both axes.

Contour lines were drawn on the graph to group species that would be similar with respect to their sustainablity. Because neither susceptibility, nor recovery alone, provide a complete index to the sustainability of species, the index is a combination of these two features. Recovery is likely to be conditionally important on susceptibility, and therefore, a multiplicative relationship between the two axes is appropriate. We assumed that this relationship is symmetrical and given this assumption, the contour lines followed the equation

$$16(y - 0.75)(x - 0.75) = 4, 9, 16, 25, 36, 49. \quad (3)$$

The impact of turtle excluder devices on elasmobranch bycatch

Data on the size of species captured in nets fitted with TEDs and with nets with standard codends were available from two sources. The crew-member observer recorded seven pairs of trawls in which one net was fitted with a TED and one had a standard codend. The TED was a Seymour TED with 110-mm bar spacing. Previous research surveys from one area of the NPF also recorded information on elasmobranchs captured in nets with and without TEDs. The TEDs were AusTEDs, NørdMore Grids, and SuperShooters; the design of these nets is detailed in Brewer et al. (1998).

The length frequency of elasmobranchs caught in nets with TEDs was compared to the length frequency of elasmobranchs caught in nets without a TED. First, species were grouped into sharks (TL measured) and rays (DW measured) for analysis. The mean length of individuals captured in nets fitted with a TED was compared with that of elasmobranchs caught in nets with a standard codend by using a one-way ANOVA. The lengths were

transformed (log (*length* + 1)) prior to analysis to normalize the data. There were sufficient data for three species of shark (*Rhizoprionodon acutus, Hemigaleus microstoma,* and *Carcharhinus dussumieri*), two stingrays (*Dasyatis leylandi* and *Himantura toshi*) and a shovel-nosed ray (*Rhynchobatus djiddensis*) to examine them separately with one-way ANOVAs.

Results

Species captured as bycatch in prawn trawls of the NPF

At least 79 species of elasmobranchs from 18 families, inhabit the NPF region (Table 3). Of these, 56 species (16 families) have been recorded in the prawn-trawl fishery bycatch (Table 3). The Carcharhinidae and Dasyatidae, the most species-rich families in the region, are the also the families for which the highest number of species are recorded in bycatch (Table 3). There are 9 families in which all species found in this region have been recorded in bycatch (Table 3).

Current catch rates

In the research and observer surveys (1996 and 1998) 44 species of elasmobranchs were recorded. The highest overall catch rates were for *Carcharhinus tilstoni, C. dussumieri, R. djiddensis,* and *H. toshi* (Table 4). These four species contributed almost 65% of the observed elasmobranch bycatch. *Carcharhinus dussumieri* and *C. tilstoni* were recorded in 20% of all trawls, *R. dijiddensis* in 14%, and *H. toshi* in 17%.

Size at first maturity and fecundity

Specimens of five species of ray were examined to assess size at first maturity and to provide estimates of fecundity (Table 5). None of the species showed a change in gonadosomatic index (GSI) or diameter of the largest egg, both of which would clearly indicate maturity. The average number of embryos was low (Table 5); most species had one or two, with the exception of *Gymnurus australis,* which had up to five embryos present.

Males of most species showed an increase in GSI with calcification of the claspers. The estimates of size at maturity for the males were lower than the estimates for females for four of the five species (Table 5). However, this finding might have been influenced by the low numbers of pregnant females sampled (Table 5). The size at maturity of the males appeared to be between 44% and 79% of the maximum size for the species.

The mean size of rays caught in bycatch ranged from 182 mm for *D. leylandi* to 1117 mm for *H. toshi* (Table 6). The mean size of sharks ranged from 541 mm for *Carcharhinus sorrah* to 1643 mm for *Rhina ancylostoma* (Table 6). For 30 species, a size at birth was available from the literature and, of these, eight species were caught in bycatch at this size (Table 6).

Where an estimate of the size at first maturity (L_m) was available for a species, an estimate could be made of the percentage of individuals captured that were mature. In species with sufficient samples sizes, the percentage of mature individuals caught ranged from <1% for *S. lewini,* to 54% for *R. acutus* (Table 6). Species such as *D. leylandi* had an average size at capture not significantly different from L_m, indicating that, on average, half the individuals caught had reached maturity before capture. Species such as *R. acutus*, with an average size less than L_m, were those for which the majority were unlikely to have bred before capture. At the other extreme were species such as *G. australis*, for which it was likely that the majority had reached maturity before capture (Table 6).

The female-to-male ratio of individuals caught was close to 1:1 for the two common species, *D. leylandi* and *C. dussumieri* (Table 6). However, other species had a range from predominantly male (e.g. *R. acutus*) to predominantly female (e.g. *H. toshi*) (Table 6).

Within-net survival

Whether an individual was alive or dead when landed on the deck was recorded for 847 animals. Overall 56% were dead after capture in the trawl and 44% were alive. Both sharks and rays showed that the probability of survival was lower for males than for females (sharks χ^2=19.7, P<0.001, rays χ^2=10.5, P=0.0012) and that survival increased with length of the individual (sharks χ^2=4.8, P=0.029, rays χ^2=11.08, P=0.0009). Two-thirds of male sharks and rays were recorded as dead after capture in the trawl (Table 7). The mean size of rays and sharks that died (sharks 684 (±10 SE) mm, rays 424 (±41 SE) mm) was smaller than the mean size of those that survived (sharks 797 (±17 SE) mm, rays 546 (±33 SE) mm). The overall percentage of individuals of a species that died varied from 10% (*R. djiddensis*) to 82% (*C. dussumieri* and *R. acutus*) (Table 7).

Assessment of the sustainability of elasmobranch species

The 56 species of elasmobranchs recorded as bycatch in the NPF were ranked on each of the criteria on the two axes (Appendices 1 and 2). The extent to which species-specific information was available varied among the criteria (Table 2). Water column position, depth range, and maximum size had species-specific information for all species. Survival and day and night catchability had little species-specific information.

Most of the criteria were not correlated (Table 8). On the susceptibility axis the strongest correlation was between diet and water column position (Table 8). However, both criteria were retained because we believed there was sufficient difference between them; the correlation coefficient (r) was only 0.67. On the recovery axis no correlations were significant (Table 8).

On the susceptibility axis (Appendix 1) the four species of Pristidae, *Atelomycterus fasciatus, Himantura jenkinsi,* and *Stegostoma fasciatum* had a rank of 1, the lowest possible rank, suggesting they were the most susceptible to capture

Table 4

The percentage of trawls in which species were caught, mean catch rate (SE=standard error), and the percentage of catch contributed by each species.

			No /km²		
Family	Species	% of trawls	Mean	SE	% of catch
Carcharhinidae	*Carcharhinus albimarginatus*	0.10	0.58	0.41	0.26
	Carcharhinus amboinensis	0.20	0.04	0.04	0.02
	Carcharhinus dussumieri	20.57	38.80	4.89	17.54
	Carcharhinus fitztroyensis	0.20	0.80	0.40	0.35
	Carcharhinus macloti	0.20	0.98	0.50	0.43
	Carcharhinus sorrah	1.67	1.47	0.57	0.65
	Carcharhinus tilstoni	19.49	44.20	5.98	20.07
	Galeocerdo cuvier	0.20	0.01	0.00	<0.01
	Negaprion acutides	0.10	0.00	0.00	<0.01
	Rhizoprionodon acutus	9.15	10.61	1.63	4.83
	Rhizoprionodon taylori	0.10	0.00	0.00	<0.01
Dasyatidae	*Amphotistius annotata*	1.97	1.56	0.41	0.74
	Dasyatis kuhlii	2.56	1.48	0.56	0.69
	Dasyatis leylandi	15.35	9.44	1.18	4.48
	Dasyatis sp. A	0.10	0.00	0.00	<0.01
	Dasyatis thetidis	0.49	0.03	0.01	0.01
	Himantura fai	0.10	0.01	0.00	<0.01
	Himantura granulata	0.20	0.01	0.01	<0.01
	Himantura jenkinsii	0.59	2.11	0.77	0.95
	Himantura sp. A	2.17	0.11	0.04	0.05
	Himantura toshi	17.72	27.85	3.10	12.84
	Himantura uarnak	0.98	1.44	0.58	0.70
	Himantura undulata	0.89	0.96	0.40	0.43
	Pastinachus sephen	3.44	0.69	0.31	0.31
	Taeniura meyeni	0.10	0.40	0.28	0.18
	Urogymnus asperrimus	0.39	0.40	0.28	0.18
Ginglymostomatidae	*Nebrius ferrugineus*	0.10	0.58	0.41	0.26
Gymnuridae	*Gymnura australis*	5.91	8.02	1.64	3.82
Hemiscylliidae	*Chiloscyllium punctatum*	5.41	11.83	1.96	5.42
	Hemigaleus microstoma	9.84	9.64	1.55	4.56
	Hemipristis elongatus	0.20	0.02	0.02	0.01
Myliobatidae	*Aetobatus narinari*	0.30	0.60	0.41	0.27
	Aetomylaeus nichofii	1.08	1.57	0.61	0.74
Orectolobidae	*Orectolobus ornatus*	0.10	0.52	0.52	0.27
Pristidae	*Anoxypristis cuspidata*	0.98	0.71	0.42	0.32
	Pristis zijsron	0.10	0.02	0.02	0.01
Rhinobatidae	*Rhinobatos typus*	0.39	0.02	0.01	0.01
Rhynchobatidae	*Rhina ancylostoma*	0.89	0.10	0.04	0.05
	Rhynchobatus djiddensis	14.27	30.87	3.39	14.26
Scyliorhinidae	*Atelomycterus fasciatus*	0.49	0.18	0.08	0.08
Sphyrnidae	*Eusphyra blochii*	0.20	0.04	0.04	0.02
	Sphyrna lewini	2.95	6.91	1.52	3.07
	Sphyrna mokarran	0.39	0.02	0.02	0.01
Stegostomatidae	*Stegostoma fasciatum*	2.17	2.17	1.02	1.10

Table 5

The estimated size (disc width) at first maturity and mean number of pups for ray species (sample size is shown in parentheses; SE=standard error).

	Size at maturity (mm)		Number of pups	
Species	Male	Female	Mean	SE
Amphotistius annotata	200 (9)	233 (8)	1.5	0.7 (2)
Dasyatis kuhlii	300 (10)	378 (6)	2	— (1)
Dasyatis leylandi	185 (103)	180 (110)	1.1	0.3 (17)
Gymnura australis	350 (29)	610 (16)	3.2	1.2 (6)
Himantura toshi	400 (31)	660 (21)	1.5	0.7 (2)

and mortality. The next 19 species had a rank of 1.15, also low. *Carcharhinus tilstoni, C. macloti, Sphyrna lewini, Prionace glauca, C. brevipinna,* and *Aetomyleus nichofii* had the highest ranks on this axis (>1.92), indicating that they were the least susceptible to capture and mortality.

On the recovery axis (Appendix 2) *Aetomyleus vespertilio, Dasyatis brevicaudatus, Pristis clavate,* and *P. pectinata* had the lowest ranks, indicating that they had the lowest capacity to recover. *Gymnura australis, H. toshi, Hemigaleus microstoma,* and *R. taylori* had the highest ranks on this axis and therefore the highest capacity to recover.

When the ranks of the species on the two axes were plotted (Fig. 2), *Dasyatis brevicaudatus, P. pectina, P. clavata, P. microdon, P. zijsron,* and *Himantura jenkinsii* ranked the lowest on the combination of the two axes, indicating that they were the least likely to be able to survive capture as bycatch. The species *Eusphyrna blochii, H. toshi, C. macloti,* and *C. tilstoni* ranked the highest on the two axes, indicating that they were the most likely to be able to survive capture as bycatch.

The impact of turtle exclusion devices on elasmobranch bycatch

Both sharks and rays taken as bycatch were significantly smaller in nets with a codend fitted with a TED (Table 9). The length frequency of the sharks and rays caught in the nets with TEDs showed a lower proportion of the larger individuals (Fig. 3). Where individual species were examined, there was a decrease in the size of *C. dussumieri* and *R. djiddensis* caught in the net with a TED (Table 9). There was no significant difference in size for *H. microstoma, A. annotata,* and *H. toshi* (Table 9). However, significantly larger individuals of *Rhizoprionodon acutus* were caught in the net with a TED (Table 9).

Discussion

Of the elasmobranch species known to inhabit this region, 71% were taken as bycatch in the NPF. The highly diverse bycatch is characteristic of tropical prawn trawl fisheries (Hall, 1999). Two critical pieces of information for assessing the impact of trawling in this region on elasmobranchs are the catch rates and survival of species.

Current catch rates

Although the bycatch was highly diverse, four species dominated the catch of the present study (*C. tilstoni, C. dussumieri, R. djiddensis,* and *H. toshi,* Table 4), occurring in 14–20% of trawls, so that one individual was seen at least every seven trawls. However, most species (75%) contributed <1% of the catch and had low catch rates (Table 4). However, even low catch rates can result in a large overall take of individuals. The fishery recorded 18,314 days of fishing in 1999 (Sharp et al.[1]) and if each day consisted of four trawls (Bishop and Sterling, 1999), 73,256 trawls (with two nets) would have been undertaken in the year. Hence for a species occurring in 1% of trawls, 733 individuals would have been caught in the year.

There are no long-term catch data available that can be examined for changes in catch rates of elasmobranch species. Although shark byproducts are recorded in NPF logbooks, the data are of limited value because they are not validated and not species-specific. Pender et al.[4] surveyed the bycatch in Northern Territory waters of the NPF during the 1980s. Rhynchobatids (71% of the elasmobranch catch), carcharhinids (12%) and dasyatids (11%) dominated the catch (Pender et al.[4]). All species recorded by Pender et al.[4] were recorded in our study. Direct comparisons of the catch rates of Pender et al.[4] with those of our study were not possible because of differences in gear, season, and region.

Most elasmobranchs caught in bycatch are small (<1000 mm). For some species, this means that most individuals have not bred before capture (Table 6) and therefore the fishery will have a greater adverse impact on the species. At least eight species were caught at sizes close to their known birth size (Table 6). This finding suggests that pupping may occur in the area of the fishery. Whether these species have restricted pupping grounds is unknown.

Within-net survival

Our estimates of within-net survival are the first for elasmobranchs in prawn trawls. The results suggest that most

Table 6

The mean, minimum (min), and maximum (max) size (TL or DW) of elasmobranch species caught in nighttime prawn trawling. The size at maturity (L_m) and at birth (pup size) are shown based on Last and Stevens (1994) or Table 5. The percentage of individuals caught that were mature (% mature) and the sex ratio are also shown. SE = standard error; n = sample size; P is the probability that the mean length at capture is different from L_m.

		Size (mm)					Sex ratio					
Family	Species	Mean	SE	Min.	Max.	n	F:M	n	L_m	P	% mature	Pup size (mm)
Carcharhinidae	*Carcharhinus albimarginatus*	850	—	—	—	1	—	—	1700	—	100	550
	Carcharhinus amboinensis	1700	—	—	—	1	—	—	2100	—	0	600
	Carcharhinus dussumieri	636	6	270	850	377	1.08	139	700	<0.001	41	350
	Carcharhinus fitzroyensis	1045	225	820	1270	2	—	—	800	>0.5	50	500
	Carcharhinus macloti	745	75	670	820	2	—	—	690	>0.5	20	450
	Carcharhinus sorrah	542	43	300	950	25	3.03	16	900	<0.001	8	500
	Carcharhinus tilstoni	794.3	9	100	1950	344	0.95	84	1200	<0.001	0.6	600
	Galeocerdo cuvier	1175	285	890	1460	2	all M	1	3000	>0.1	0	500
	Negaprion acutidens	2600	—	—	—	1	—	—	2200	—	—	500
	Rhizoprionodon acutus	689	14	280	960	140	0.56	81	750	<0.001	54	—
	Rhizoprionodon taylori	546	—	—	—	1	all F	1	400	—	100	250
Dasyatidae	*Amphotistius annotata*	211.4	12	140	452	25	1.43	3	200	>0.5	24	—
	Dasyatis kuhlii	297.3	12	190	400	24	4.00	10	300	>0.5	8	160
	Dasyatis leylandi	182.2	3	110	400	206	1.05	162	180	>0.2	46	110
	Dasyatis sp. A	350	—	—	—	1	—	—	360	—	0	—
	Dasyatis thetidis	1162	129	800	1420	5	all M	1	—	—	—	350
	Himantura fai	1900	—	—	—	1	—	—	—	—	—	550
	Himantura granulata	960	—	—	—	1	—	—	—	—	—	280
	Himantura jenkinsii	890	150	300	1140	5	all M	1	—	—	—	—
	Himantura sp. A	350	65	80	1800	57	all F	12	—	—	—	—
	Himantura toshi	456	11	150	1330	235	4.17	52	400	<0.001	12	200
	Himantura uarnak	1055	132	290	1600	12	all F	2	—	—	—	280
	Himantura undulata	1117	131	400	1500	7	all F	1	—	—	—	200
	Pastinachus sephen	1076	53	450	2000	43	3.03	12	—	—	—	180
	Taeniura meyeni	1300	—	—	—	1	—	—	—	—	—	350
	Urogymnus asperrimus	850	106	530	1150	5	all M	2	—	—	—	—
Ginglymostomatidae	*Nebrius ferrugineus*	2400	—	—	—	1	—	—	2250	—	100	400
Gymnuridae	*Gymnura australis*	462	19	120	860	87	2.00	42	350	<0.001	24	—
Hemigaleidae	*Hemigaleus microstoma*	609	19	250	950	152	0.68	91	600	>0.5	47	300
	Hemipristis elongata	1340	190	1150	1530	2	all F	1	1100	>0.5	50	520
Hemiscylliidae	*Chiloscyllium punctatum*	668	23	230	1000	63	2.50	7	700	<0.001	52	170
Myliobatidae	*Aetobatus narinari*	625	125	500	750	2	all F	1	—	—	—	260
	Aetomylaeus nichofii	437	42	240	720	11	all F	3	—	—	—	170
Pristidae	*Anoxypristis cuspidata*	1930	193	1240	2550	8	all F	1	—	—	—	—
Rhinobatidae	*Rhinobatos typus*	1953	188	1500	2340	4	—	—	—	—	—	—
Rhynchobatidae	*Rhina ancylostoma*	1643	112	1010	2090	9	0.33	3	—	—	—	—
	Rhynchobatus djiddensis	869	36	230	2650	187	4.76	35	1100	<0.001	8	—
Scyliorhinidae	*Atelomycterus fasciatus*	300	0	300	300	2	—	—	320	—	0	—
Sphyrnidae	*Eusphyra blochii*	990	320	670	1310	2	—	—	1080	>0.5	50	450
	Sphyrna lewini	832	54	400	2400	37	all F	3	1400	<0.001	3	450
	Sphyrna mokarran	1780	457	400	2400	3	1.00	2	2100	>0.5	33	650
Stegostomatidae	*Stegostoma fasciatum*	1305	82	400	2000	26	0.80	3	1700	<0.001	23	200

Table 7

The percentage of elasmobranchs that died within the trawl net, recorded on research and crew-member observer surveys. "Combined sharks" refers to all species where total length was recorded; "combined rays" refers to all species where disc width was recorded; n = number of specimens measured.

		% dead					
Family	Taxa	Female	n	Male	n	Overall	n
	combined sharks	23	149	66	59	61	639
	combined rays	56	360	67	279	40	208
Carcharhinidae	*Carcharhinus dussumieri*	48	207	58	114	52	321
	Carcharhinus sorrah	73	15	50	8	65	23
	Carcharhinus tilstoni	78	40	85	33	82	73
	Rhizoprionodon acutus	75	44	86	72	82	116
Dasyatidae	*Dasyatis leylandi*	27	22	95	19	59	41
	Himantura toshi	43	40	78	18	53	58
Gymnuridae	*Gymnura australis*	31	26	75	8	41	34
Hemigaleidae	*Hemigaleus microstoma*	44	29	64	39	62	68
Rhynchobatidae	*Rhynchobatus djiddensis*	21	24	20	5	10	59

Table 8

The correlations between the criteria on 1) the susceptibility axis and 2) the recovery axis. * indicates significance at $P < 0.05$.

Susceptibility	Survival	Range	Day and night catchability	Diet	Depth range
Water column position	0.07	–0.18	0.13	0.67*	0.07
Survival		0.48*	0.07	–0.11	–0.00
Range			0.25	0.06	0.09
Day and night catchability				–0.15	0.04
Diet					0.05

Recovery	Maximum size	Removal rate	Annual fecundity	Mortality index
Probability of breeding	0.07	0.25	0.16	0.08
Maximum size		–0.22	–0.25	0.17
Removal rate			–0.27	0.21
Annual fecundity				0.12

sharks and rays, particularly the smaller individuals, die within the trawl net (56%). The lower survival rates of male individuals is possibly because the males of most elasmobranch species are smaller than the females. The rhynchobatid *R. djiddensis* had a higher survival rate (90%) than most other species, whereas the lowest survival rate was seen in *C. tilstoni* and *R. acutus* (18%). Although the larger elasmobranchs appeared to have a higher within-net survival, in the commercial fishery these were the very individuals killed for their fins and therefore their mortality was ultimately higher than that predicted by their size alone. In 2001 the NPF introduced an industry-initiated ban on all shark products, so that the only mortality these species are subject to is that caused by the capture process. Differences between species in survival rates may influence changes in the relative abundance of species.

Assessment of the sustainability of elasmobranch species

Elasmobranchs, in general, are more susceptible to overfishing than are bony fishes, but there is likely to be a range of sensitivities among the species (Walker, 1998; Stevens et al., 2000). The process we applied in our study allowed us to examine these different sensitivities and to highlight those species whose populations were most likely to be affected by the NPF. The process was designed to deal with the high diversity of the bycatch and the

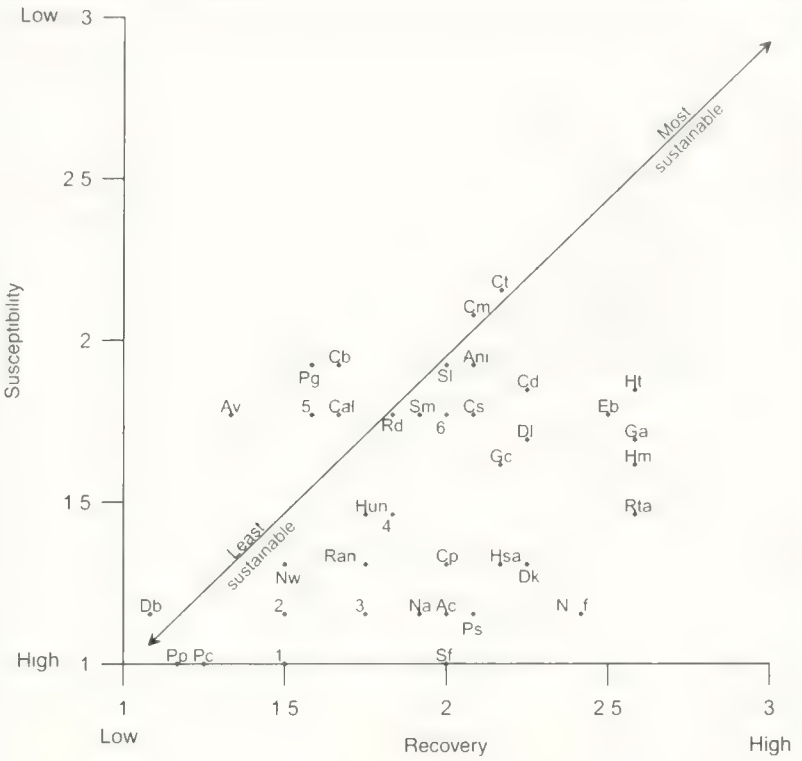


Figure 2

The ranking of elasmobranch species with respect to criteria that reflect their susceptibility to capture and mortality due to prawn trawling and their capacity to recover after depletion by trawling. These factors combine to reflect the relative ability of species to sustain capture as prawn trawl bycatch in the northern prawn fishery and therefore their relative priority with respect to research and management. Numbers refer to species combinations that fall together on the graph. (1=Hj, Pm, Pz; 2=Ca, Cle, Dt, Gsa, Ssa, Tm; 3=Af, Dsa, Hf, Hg Hua, Oo, Rty, Ua; 4=Cf, Aa; 5=Ana, Cli; 6=Rac, He). Explanations of the abbreviations for species are given in Table 3.

paucity of information available for most species. Our process was similar to that used by the International Union for the Conservation of Nature and Natural Resources (IUCN) red lists (IUCN, 1995) that categorize species with respect to the threat of extinction worldwide. The IUCN uses criteria on the extent of population decrease, area of occurrence, percentage of population that is mature, and the probability of extinction (IUCN, 1995). The IUCN criteria have been modified for application to marine fishes and to smaller geographic scales (Musick, 1998). With respect to elasmobranchs, several authors have examined the variable resilience of species to fishing pressure. These approaches have focused on life history characteristics that influence the recovery of populations, including reproductive and growth parameters (reviewed by Stevens et al., 2000). Our process is similar to these but focuses at the level of an individual fishery, incorporating fishery-specific information on the susceptibility of species to the fishery. Of significant importance with all methods is the ability to calculate the range of parameters required for a large number of species (Stevens et al., 2000). The semi-quantitative method used in our study maximizes what can be determined from the data available and enables consistency across the species. The criteria include characteristics that influence the probability of extinction of a species and its sensitivity to overfishing (McKinney, 1997; Carlton et al., 1999; Roberts and Hawkins, 1999; Stevens et al., 2000). Our analysis provides a process for highlighting gaps in information and for prioritizing species for future management and research. This process does not replace traditional methods of population assessment but provides a rapid assessment of the species, so that traditional methods can be focused on the high-risk species.

The species that were least likely to be sustainable in the bycatch of the NPF were *D. brevicaudatus, P. pectinata, P. clavata, P. microdon, P. zijsron,* and *Himantura jenkinsii* (Fig. 3). The pristids and *H. jenkinsii* had ranks of 1 on the susceptibility axis, the lowest possible rank, and *D. brevicaudatus* ranked 1.15 (Appendix 1). These species are demersal, are rare in the bycatch, and at least for the pristids (which have restricted depth distributions) are likely to be rare. Nothing is known about their sur-

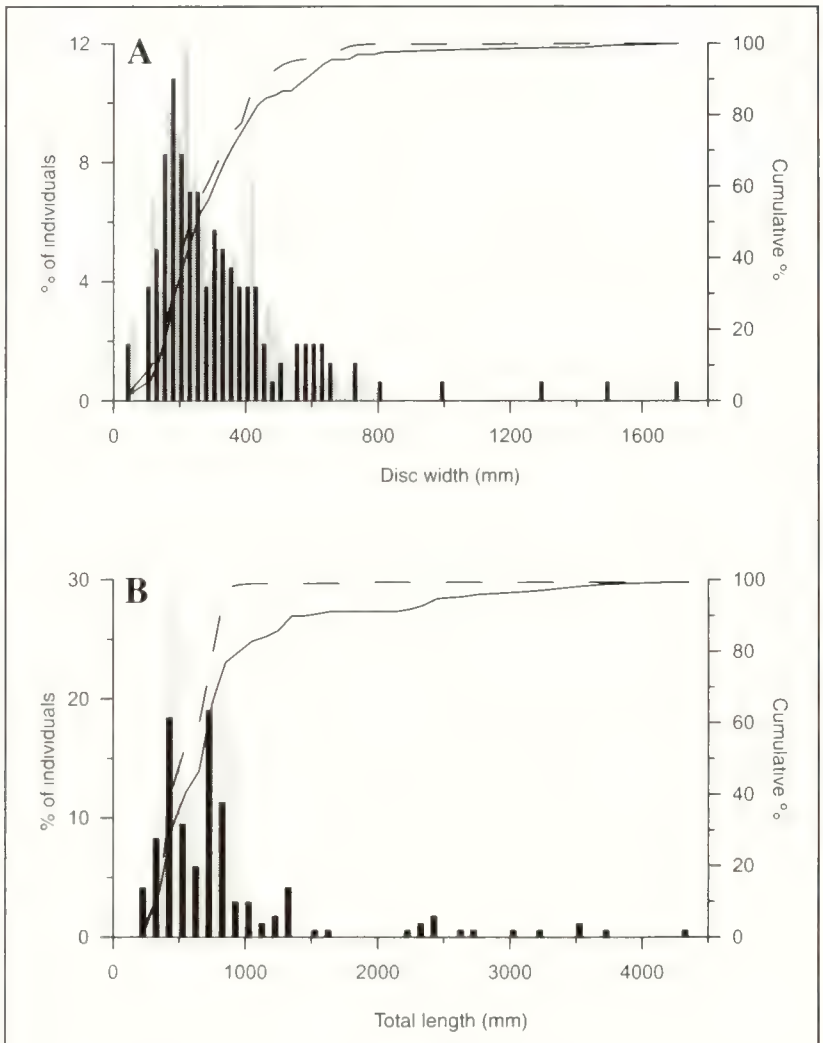


Figure 3

The length frequency and cumulative length frequency of rays (**A**) and sharks (**B**) caught in nets with a standard codend (black columns and solid line) and nets with a TED (grey columns and broken line).

vival. Their diets include benthic organisms and are likely to include commercial prawns; their range and day and night catchability is unknown. The combination of these factors means that these species are likely to occur in trawl grounds and that they are highly susceptible to capture and mortality due to trawlers. The recovery capacity of populations of these species is also low (Appendix 2). The rarity of the species in the bycatch means that no data are available to estimate the probability of breeding before capture, removal rate, total biomass, or the mortality index for most of these species, and they therefore received ranks of 1 for these criteria. In general these are large animals and are therefore likely to have slower recovery rates for their population than those of smaller species. The annual fecundity was low for all species.

The pristids are the focus of increasing international concern because their populations are declining worldwide (Stevens et al. 2000). They are rarely seen today in areas where they were previously abundant (Simpfendorfer, 2000). This decrease in pristid populations has resulted in four species being listed on the IUCN 1996 red list (Bailie and Groombridge, 1996). Of the species studied in our study, *P. pectinata* and *P. microdon* are listed as endangered. Recent demographic analysis of pristid populations has indicated that their recovery will take several decades even if they are given effective conservation (Simpfendorfer, 2000).

In comparison, the species that were most likely to be able to sustain capture in the bycatch of the NPF were *H. toshi, E. blockii, C. macloti,* and *C. tilstoni.* These species had a lower susceptibility to capture and mortality due to trawling (Appendix 1). With the exception of *H. toshi*, these are pelagic species and there is little likelihood of their capture in prawn trawls. For the species for which

Table 9

The mean size of elasmobranch species caught in nets with codends fitted with TEDs and with standard codends, and the ANOVA results from the comparison of these nets. "Combined sharks" refers to all species where total length was recorded; "combined rays" refers to all species where disc width was recorded. SE = standard error; n = number of trawls.

		Size (mm)			ANOVA results		
Species	Codend	mean	SE	n	F	df	P
Combined sharks	standard	887	59	168	4.25	1,569	0.0398
	TED	596	36	269			
Combined rays	standard	330	19	157	26.77	1,435	<0.0001
	TED	286	7	414			
Carcharhinus dussumieri	standard	844.4	96.4	60	26.88	1,139	<0.0001
	TED	489.1	13.8	81			
Rhizoprionodon acutus	standard	636.9	34.2	45	7.15	1,134	0.0084
	TED	724.2	17.4	91			
Hemigaleus microstoma	standard	708.9	148.5	23	2.77	1,79	0.0988
	TED	508.0	19.9	58			
Amphotistius annotata	standard	206.4	31.1	50	2.97	1,200	0.4395
	TED	169.8	3.4	156			
Himantura toshi	standard	371.0	19.4	51	0.60	1,200	0.4395
	TED	351.6	9.7	151			
Rhynchobatus djiddensis	standard	1076.9	125.6	19	20.81	1,41	<0.0001
	TED	611.6	32.3	24			

data were available, their survival was higher in trawls. The depth range of the species was wide and their catch rates during the day were the same as or higher than at night. This range provides partial refuge from the nighttime commercial trawling. The data available suggest that their recovery capacity is higher than that of most elasmobranch species (Appendix 2). Individuals of most of these species are likely to have bred before capture and they are smaller. These species were common in the bycatch, and estimates of their removal rate (which was low) and their mortality index (average) were therefore easy to determine. However, all species had low annual fecundities.

This assessment of the elasmobranch bycatch is an important first step in ensuring their sustainability because it provides a focus for future research and management. The current ranking is constrained, however, by the available data and by the assumptions outlined in the "Methods" section. The effect of the lack of species-specific information on the ranks should be taken into account because it may reduce the rank of some species. The application of our assessment has highlighted important information gaps, which should be the focus of research, particularly for the species that are least likely to be sustainable.

It is also important that the assessment of the sustainability of elasmobranch species is extended to include the impact of other fisheries in the region. There are, for instance, fisheries targeting sharks, as well as other fisheries that capture elasmobranchs as bycatch. Because elasmobranch species may have a wide distribution range, their populations could be impacted by several fisheries, which might create an unsustainable status for the population overall. For example, the pristids are likely to be impacted by the inshore and estuarine gillnet fisheries in this region.

The results of our analysis, it is to be hoped, will help in the management of elasmobranch species and in earmarking the least sustainable of these species. Future management may include the use of exclusion devices (TEDs and BRDs), closures, or further limits on retaining shark products. The compulsory introduction of TEDs and BRDs into the NPF in 2000 is likely to affect catch rates of elasmobranchs. The TEDs have the potential to exclude large individuals. However, the majority of elasmobranchs caught are <1000 mm (Fig. 3) and may escape through TEDs. The effectiveness of TEDs will depend on their configuration (particularly the width between the bars) and the size and shape of the bycatch species. *Rhynchobatus djiddensis,* a large, broad species, appeared to be excluded well by TEDs (Table 9). In comparison, the smaller rays and small, slim sharks were not excluded well (Fig. 3, Table 9). With the introduction of TEDs to the fishery, species-specific exclusion rates should be monitored so that these can be taken into account in assessing the sustainability of a species. Juveniles of many elasmobranch species are still likely to be captured and their capture could potentially have a large impact on their respective populations. The TEDs may also be ineffective for species, such as the pristids, that may tangle their saw in the net or the TED. Species and the life stages of species, for which exclusion devices are not effective, may require different management strategies, such as marine protected areas.

This research is the first large-scale assessment of its kind on elasmobranch bycatch. The results highlight the diversity of elasmobranch bycatch in the NPF and the species that are least likely to be sustainable. We have also highlighted the limited information available for making this assessment. However, our method was designed to maximize the use of the limited information. The process we have used is applicable to other fisheries and also across fisheries, particularly where bycatch diversity is high.

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Appendix 1

The ranking of elasmobranch species that occurred in the bycatch of the northern prawn fishery with respect to criteria that influence their susceptibility to capture and mortality due to prawn trawls. The weights of the criteria are shown in parentheses; * indicates where species-specific information was not available. The information was obtained from Compagno (19984a; 1984b), Last and Stevens (1994), and Froese and Pauly[6].

		Criteria						
Family	Species	Water column position (3)	Survival (3)	Range (2)	Day and night catchability (2)	Diet (2)	Depth range (1)	Susceptibility ranking
Dasyatidae	*Himantura jenkinsii*	1	1*	1	1*	1*	1	1.00
Pristidae	*Pristis clavata*	1	1*	1*	1*	1*	1	1.00
Pristidae	*Pristis microdon*	1	1*	1*	1*	1*	1	1.00
Pristidae	*Pristis pectinata*	1	1*	1*	1*	1*	1	1.00
Pristidae	*Pristis zijsron*	1	1*	1	1*	1*	1	1.00
Stegostomatidae	*Stegostoma fasciatum*	1	1*	1*	1	1	1	1.00
Scyliorhinidae	*Atelomycterus fasciatus*	1	1*	1	1*	1*	3	1.15
Carcharhinidae	*Carcharhinus amboinensis*	1	1*	1	1*	1	3	1.15
Carcharhinidae	*Carcharhinus leucas*	1	1*	1*	1*	1	3	1.15
Dasyatidae	*Dasyatis brevicaudatus*	1	1*	1*	1*	1*	3	1.15
Dasyatidae	*Dasyatis* sp. A	1	1*	1	1*	1*	3	1.15
Dasyatidae	*Dasyatis thetidis*	1	1*	1	1*	1*	3	1.15
Scyliorhinidae	*Galeus* sp. A	1	1*	1*	1*	1*	3	1.15
Dasyatidae	*Himantura fai*	1	1*	1	1*	1*	3	1.15
Dasyatidae	*Himantura granulata*	1	1*	1	1*	1	3	1.15
Dasyatidae	*Himantura uarnak*	1	1*	1*	1*	1*	3	1.15
Ginglymostomatidae	*Nebrius ferrugineus*	1	1*	1	1*	1	3	1.15
Carcharhinidae	*Negaprion acutidens*	1	1*	1	1*	1	3	1.15
Orectolobidae	*Orectolobus ornatus*	1	1*	1	1	1	3	1.15
Rhinobatidae	*Rhinobatos typus*	1	1*	1	1*	1*	3	1.15
Squatinidae	Squatina *sp. A*	1	1*	1*	1*	1*	3	1.15
Dasyatidae	*Taeniura meyeni*	1	1*	1	1*	1*	3	1.15
Dasyatidae	*Urogymnus asperrimus*	1	1*	1	1*	1*	3	1.15
Pristidae	*Anoxypristis cuspidata*	1	1*	1*	2	1*	1	1.15
Dasyatidae	*Pastinachus sephen*	1	1*	2	1*	1	1	1.15
Hemiscyllidae	*Chiloscyllium punctatum*	1	1*	2	1	1	3	1.31
Dasyatidae	*Dasyatis kuhlii*	1	1*	2	1	1*	3	1.31
Dasyatidae	*Himantura* sp. A	1	1*	2	1*	1*	3	1.31
Narcinidae	*Narcine westraliensis*	1	1*	1*	1*	2	3	1.31
Rhynchobatidae	*Rhina ancylostoma*	1	1*	2	1	1	3	1.31
Carcharhinidae	*Carcharhinus fitztroyensis*	3	1*	1	1*	1	1	1.46
Dasyatidae	*Amphotistius annotata*	1	1*	2	2	1*	3	1.46
Dasyatidae	*Himantura undulata*	1	1*	2	2	1*	3	1.46
Carcharhinidae	*Rhizoprionodon taylori*	1	1*	1	3	1	3	1.46
Carcharhinidae	*Galeocerdo cuvier*	3	1*	1	1*	1	3	1.62
Hemiscyllidae	*Hemigaleus microstoma*	1	1	3	1*	2	3	1.62
Dasyatidae	*Dasyatis leylandi*	1	2	3	1	1	3	1.69
Gymnuridae	*Gymnura australis*	1	2	3	2	1*	1	1.69
Carcharhinidae	*Carcharhinus sorrah*	3	1	2	1*	1	3	1.77
Carcharhinidae	*Rhizoprionodon acutus*	1	1	3	3	1	3	1.77
Rhynchobatidae	*Rhynchobatus djiddensis*	1	3	2	1*	1*	3	1.77

continued

Appendix 1 (continued)

		Criteria						
Family	Species	Water column position (3)	Survival (3)	Range (2)	Day and night catchability (2)	Diet (2)	Depth range (1)	Susceptibility ranking
Myliobatidae	*Aetobatus narinari*	3	1*	1	1*	2	3	1.77
Myliobatidae	*Aetomylaeus vespertilio*	3	1*	1*	1*	2*	3	1.77
Carcharhinidae	*Carcharhinus albimarginatus*	3	1*	1	1*	2	3	1.77
Hemiscylliidae	*Hemipristis elongatus*	3	1*	1	1*	2	3	1.77
Sphyrnidae	*Sphyrna mokarran*	3	1*	1	1*	2	3	1.77
Carcharhinidae	*Carcharhinus limbatus*	3	1	1*	1*	3	1	1.77
Sphyrnidae	*Eusphyra blochii*	3	1*	1	2	1	3	1.77
Carcharhinidae	*Carcharhinus dussumieri*	1	2	2	3	1	3	1.85
Dasyatidae	*Himantura toshi*	1	2	3	2	1	3	1.85
Myliobatidae	*Aetomyleus nichofii*	3	1*	2	1	2*	3	1.92
Carcharhinidae	*Carcharhinus brevipinna*	3	1*	1*	1*	3	3	1.92
Carcharhinidae	*Prionace glauca*	3	1*	1*	1*	3	3	1.92
Sphyrnidae	*Sphyrna lewini*	3	1*	1*	1*	3	3	1.92
Carcharhinidae	*Carcharhinus macloti*	3	1*	1	3	2	3	2.08
Carcharhinidae	*Carcharhinus tilstoni*	3	2	2	2	1	3	2.15

Appendix 2

The ranking of elasmobranch species that occurrred in the bycatch of the northern prawn fishery with respect to criteria that reflect their capacity to recover after depletion by trawling. The weights of the criteria are shown in parentheses; * indicates where species-specific information was not available. The information was obtained from Compagno (1984a; 1984b), Last and Stevens (1994), and Froese and Pauly[6].

		Criteria					
Family	Species	Probability of breeding (3)	Maximum size (3)	Removal rate (3)	Annual fecundity (2)	Mortality index (1)	Recovery ranking
Dasyatidae	*Dasyatis brevicaudatus*	1	1	1*	1	2	1.08
Pristidae	*Pristis pectinata*	1*	1	1*	2	1*	1.17
Pristidae	*Pristis clavata*	1*	2	1*	1*	1*	1.25
Myliobatidae	*Aetomylaeus vespertilio*	1*	2	1*	1*	2	1.33
Dasyatidae	*Taeniura meyeni*	1	1	3	1	1	1.50
Dasyatidae	*Himantura jenkinsii*	1*	2	2	1*	1	1.50
Carcharhinidae	*Carcharhinus amboinensis*	1	2	1	2	2	1.50
Carcharhinidae	*Carcharhinus leucas*	1	3	1*	1	1	1.50
Scyliorhinidae	*Galeus* sp. A	1*	3	1*	1*	1*	1.50
Narcinidae	*Narcine westraliensis*	1*	3	1*	1*	1*	1.50
Pristidae	*Pristis microdon*	1*	3	1*	1*	1*	1.50
Squatinidae	*Squatina* sp. A	1*	3	1*	1*	1*	1.50
Carcharhinidae	*Prionace glauca*	1*	2	1*	3	1*	1.58
Myliobatidae	*Aetobatus narinari*	1*	1	3	1	2	1.58
Carcharhinidae	*Carcharhinus limbatus*	1*	3	1*	1	2	1.58
Carcharhinidae	*Carcharhinus albimarginatus*	1*	2	2	2	1*	1.67
Carcharhinidae	*Carcharhinus brevipinna*	1*	3	1*	2	1*	1.67
Dasyatidae	*Dasyatis thetidis*	1*	2	3	1*	1	1.75
Pristidae	*Pristis zijsron*	1*	2	3	1*	1*	1.75
Dasyatidae	*Himantura fai*	1*	2	3	1*	1*	1.75
Dasyatidae	*Himantura granulata*	1	2	3	1*	1*	1.75
Dasyatidae	*Himantura uarnak*	1	2	3	1*	1	1.75
Dasyatidae	*Himantura undulata*	1*	2	3	1*	1	1.75
Orectolobidae	*Orectolobus ornatus*	1*	2	3	1*	1*	1.75
Dasyatidae	*Urogymnus asperrimus*	1	2	3	1	1	1.75
Scyliorhinidae	*Atelomycterus fasciatus*	2	2	2	1	1	1.75
Dasyatidae	*Dasyatis* sp. A	2	3	1	1*	1*	1.75
Dasyatidae	*Amphotistius annotata*	2*	1	3	1*	2	1.83
Rhynchobatidae	*Rhynchobatus djiddensis*	1	2	3	1*	2	1.83
Carcharhinidae	*Carcharhinus fitztroyensis*	2	2	2	1	2	1.83
Sphyrnidae	*Sphyrna mokarran*	2	1	3	2*	1	1.92
Carcharhinidae	*Negaprion acutidens*	3	2	1	2	1*	1.92
Rhynchobatidae	*Rhina ancylostoma*	1*	3	3	1*	1	2.00
Rhinobatidae	*Rhinobatos typus*	1*	3	3	1*	1	2.00
Pristidae	*Anoxypristis cuspidata*	1	3	3	1	1*	2.00
Hemiscylliidae	*Chiloscyllium punctatum*	1*	3	3	1*	1	2.00
Hemiscylliidae	*Hemipristis elongatus*	2	2	3	1	1	2.00
Carcharhinidae	*Rhizoprionodon acutus*	1	3	3	1	1	2.00
Stegostomatidae	*Stegostoma fasciatum*	2*	2	3	1*	1	2.00
Sphyrnidae	*Sphyrna lewini*	1*	2	3	2*	2*	2.00
Myliobatidae	*Aetomylaeus nichofii*	1*	3	3	1	2	2.08
Carcharhinidae	*Carcharhinus macloti*	2	2	3	1	2	2.08

continued

Appendix 2 (continued)

Family	Species	Criteria					
		Probability of breeding (3)	Maximum size (3)	Removal rate (3)	Annual fecundity (2)	Mortality index (1)	Recovery ranking
Carcharhinidae	*Carcharhinus sorrah*	1	3	3	1*	2	2.08
Dasyatidae	*Pastinachus sephen*	3	1	3	1*	2	2.08
Carcharhinidae	*Galeocerdo cuvier*	2	1	3	3	2	2.17
Dasyatidae	*Himantura* sp. A	1*	3	3	1*	3	2.17
Carcharhinidae	*Carcharhinus tilstoni*	1	3	3	1	3	2.17
Carcharhinidae	*Carcharhinus dussumieri*	3	2	3	1	1	2.25
Dasyatidae	*Dasyatis kuhlii*	2	3	3	1	1*	2.25
Dasyatidae	*Dasyatis leylandi*	2	3	3	1*	1*	2.25
Ginglymostomatidae	*Nebrius ferrugineus*	3	2	3	2	1*	2.42
Sphyrnidae	*Eusphyra blochii*	2	3	3	2	2	2.50
Gymnuridae	*Gymnura australis*	3	3	3	1	2	2.58
Dasyatidae	*Himantura toshi*	3	3	3	1	2	2.58
Carcharhinidae	*Rhizoprionodon taylori*	3	3	3	1	2	2.58
Hemiscylliidae	*Hemigaleus microstoma*	2	3	3	2	3	2.58

Age and growth of the swordfish (*Xiphias gladius* L.) in the waters around Taiwan determined from anal-fin rays

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Abstract—Age and growth of the swordfish (*Xiphias gladius*) in Taiwan waters was studied from counts of growth bands on cross sections of the second ray of the first anal fin. Data on lower jaw fork length and weight, and samples of the anal fin of male and female swordfish were collected from three offshore and coastal tuna longline fishing ports on a monthly basis between September 1997 and March 1999. In total, 685 anal fins were collected and 627 of them (293 males and 334 females) were aged successfully. The lower jaw fork lengths of the aged individuals ranged from 83.4 to 246.6 cm for the females and from 83.3 to 206 cm for the males.

The radii of the fin rays and growth bands on the cross sections were measured under a dissecting microscope equipped with an image analysis system. Trends in the monthly marginal increment ratio indicated that growth bands formed once a year. Thus, the age of each fish was determined from the number of visible growth bands. Two methods were used to estimate and compare the standard and the generalized von Bertalanffy growth parameters for both males and females. The nonlinear least square estimates of the generalized von Bertalanffy growth parameters in method II, in which a power function was used to describe the relationship between ray radius and LJFL, were recommended as most acceptable. There were significant differences in growth parameters between males and females. The growth parameters estimated for females were the following: asymptotic length (L_∞) = 300.66 cm, growth coefficient (K) = 0.040/yr, age at zero length (t_0) = –0.75 yr, and the fitted fourth parameter (m) = –0.785. The growth parameters estimated for males were the following: asymptotic length (L_∞) = 213.05 cm, growth coefficient (K) = 0.086/yr, age at zero length (t_0) = –0.626 yr, and the fitted fourth parameter (m) = –0.768.

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The swordfish (*Xiphias gladius* L.) is a cosmopolitan species found in the tropical, subtropical, and temperate waters of the world's oceans and adjacent seas (Sakagawa, 1989). In the Pacific Ocean, swordfish is generally distributed from Asia to the Americas between 50°N and 50°S (Bartoo and Coan, 1989). In the waters of Taiwan, the swordfish is an incidental bycatch of the offshore tuna longline and harpoon fisheries. Both fisheries contributed an estimated 1528 metric tons (99%) to the total swordfish landings from Taiwan waters in 1999.

Information on age and growth of fishes is a central element in fishery management (Brothers, 1983). Measurement of the age of the fish provides the key variable of time needed to estimate life history and biology factors, such as mortality and growth. Mortality and growth-rate models provide quantitative information on the status of fish stocks and at the same time may be used in more sophisticated models, such as yield-per-recruit analyses and cohort analyses (Powers, 1983), which will directly contribute to the rational exploitation of fish resources, as well as to the development of proper management plans.

Most age determination studies of swordfish have dealt with Atlantic populations and have used different hard parts, such as anal-fin rays (Berkeley and Houde, 1983; Wilson and Dean 1983; Prince et al., 1988; Ehrhardt, 1992; Esteves et al., 1995; Ehrhardt et al., 1996), otolith (Radtke and Hurley, 1983; Wilson and Dean, 1983; Esteves et al., 1995), and vertebrae (Esteves et al., 1995). In contrast, only a few attempts have been made to determine the age of swordfish in the Pacific Ocean. Yabe et al. (1959) estimated the growth of swordfish caught in the western North Pacific (140°–160°E) by longline during the period from 1948 to 1956 using the modal analysis of length frequencies. Castro-Longoria and Sosa-Nishizaki (1998) compared the age estimates of swordfish caught by drift gillnet vessels off Baja California from 1992 to 1993 based on otolith microstructure and cross sections of the second ray from the first anal fin, and highly recommended the use of cross sections of the second ray to determine the ages of swordfish in the Pacific Ocean. Uchiyama et al. (1998) evaluated various hard parts (including rays of the first dorsal and first anal fins, vertebrae, and sagittae) for aging swordfish in the central North Pacific by Hawaii longline fishery from 1991 to 1993, and provided preliminary estimates of length-at-age.

The objectives of our study were to estimate the age and growth of swordfish by counting the growth rings on the cross sections of the second ray of the first anal fin and to compare the generalized growth function proposed by Richards (1959) with the standard von Bertalanffy model for representing the best growth model of swordfish around Taiwan waters. The information is crucial because it will allow the age composition of the catch to be determined, which in turn will allow the status of the swordfish stock in the

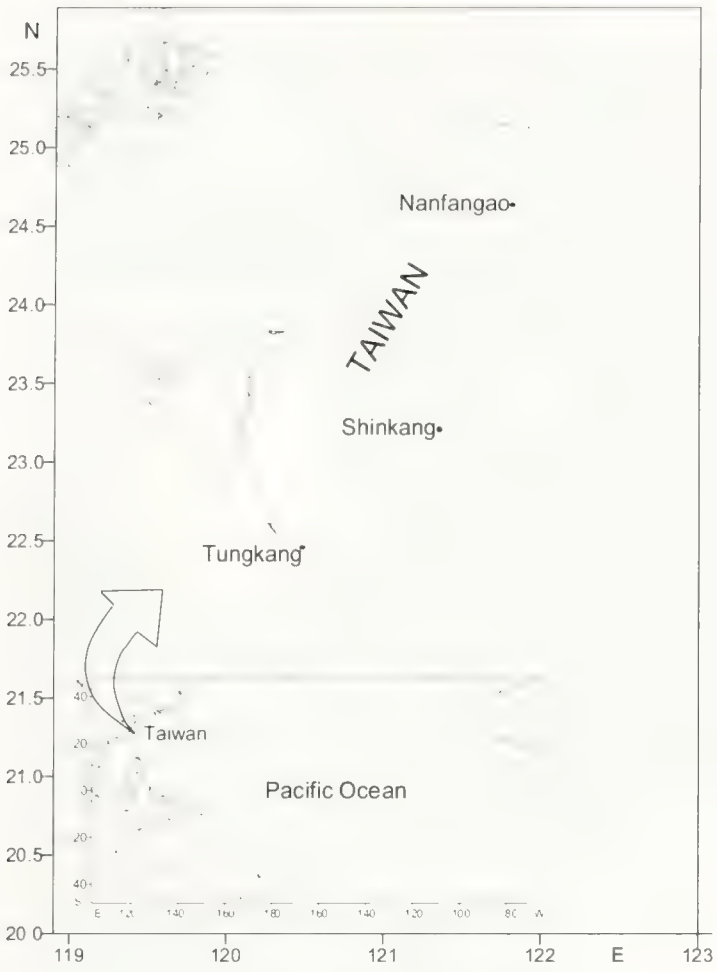

Figure 1

Three fishing ports in Taiwan where the swordfish anal-fin ray samples were collected in this study.

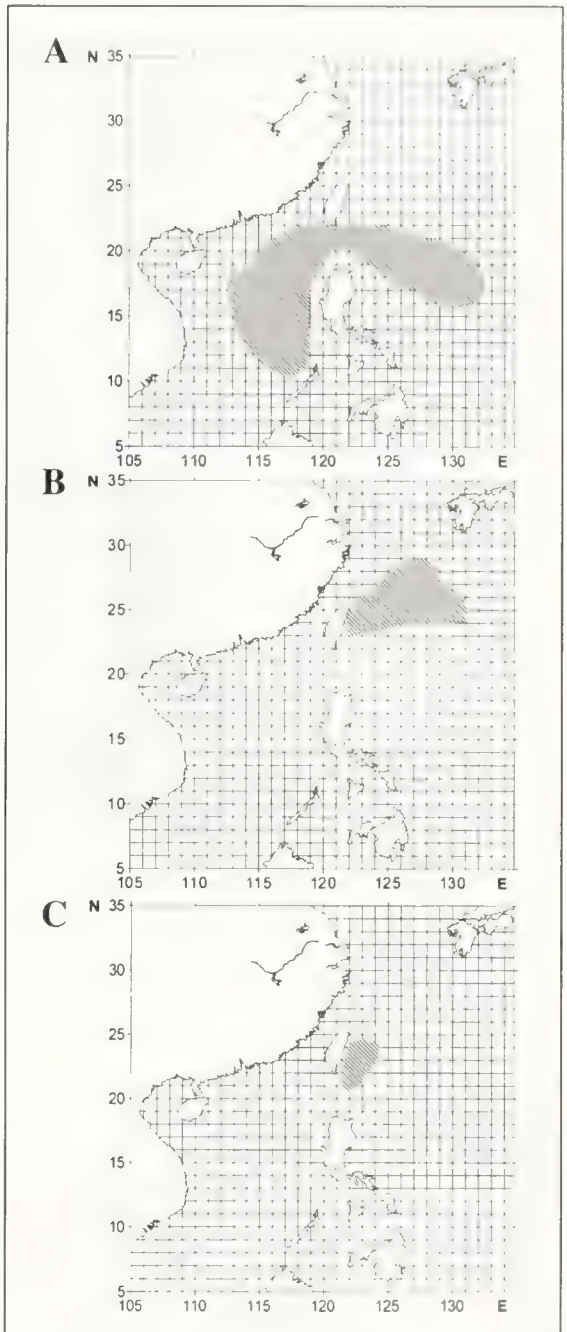

Figure 2

The fishing grounds (oblique dot lines) of the longline and harpoon fishing boats based in Tungkang (**A**), Nanfangao (**B**), and Shinkang (**C**) fishing ports.

waters around Taiwan to be assessed by using yield-per-recruit and sequential population analyses.

Material and methods

Data on lower jaw fork length (LJFL) and weight, and samples of the first anal fin of male and female swordfish were collected from three offshore tuna longline and harpoon fishing ports (Fig. 1) on a monthly basis between September 1997 and March 1999. The fishing grounds for those vessels are shown in Figure 2. In total, 769 LJFLs and 685 anal fins were collected. The anal fins were frozen for approximately one month before being thawed and boiled to remove the tissue and to separate the second rays. Three cross sections ranging in thickness from 0.5 to 0.75 to 1.0 mm were taken successively along the length of each ray with a low-speed "ISOMET" saw (model no. 11-1280) and diamond wafering blades, at a location equivalent to 1/2 of the maximum width of the condyle base measured above the line of maximum condyle width (Fig. 3) (Ehrhardt, 1992; Ehrhardt et al., 1996). The sections were immersed in 95% ethanol for several minutes, placed in a labeled (with sampling date and a number) small plastic case to air dry, and then stored for later reading. Anal-fin ray sections were then taken from the small cases randomly and examined under a dissecting microscope (model: Leica MZ 6) with transmitted light at various

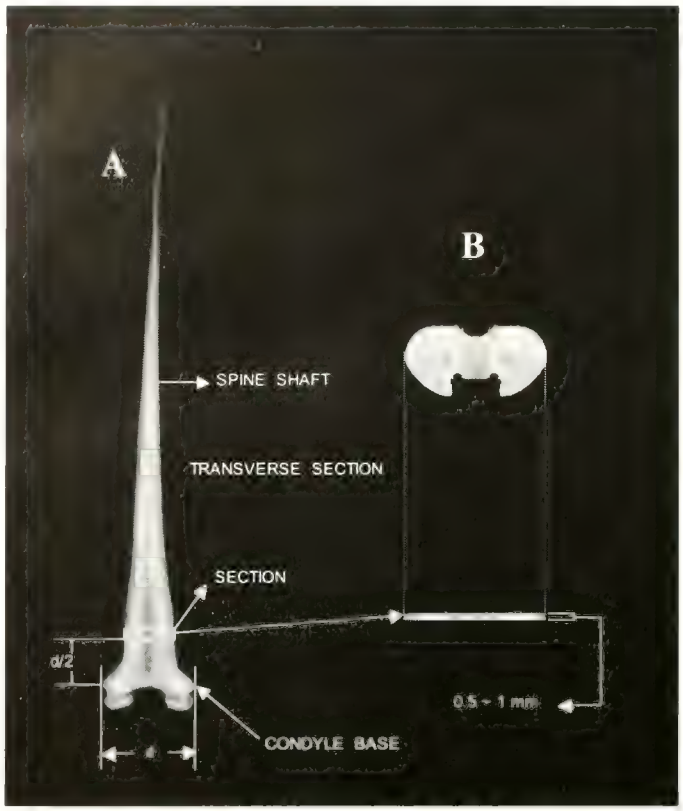

Figure 3

The second ray of the first anal fin showing the location of the cross section at a distance equal to a half of the width of the condyle base above the base (**A**), and a section of the second ray of the first anal fin (**B**).

magnifications from 8× to 16× depending on the size of the section. The clearest one of the three sections from each fin ray was read three times by one reader about one to three months apart with no knowledge of fish length. The precision of readings was evaluated as the average percent error (APE, Beamish and Fournier, 1981) and coefficient of variation (CV, Campana et al., 1995, 2001). For those sections resulting in three different readings, each section was reread by two to three readers simultaneously. Specimens whose age estimates still disagreed were omitted from further analyses.

The images of the anal-fin ray sections were captured by using an Image Analysis Software package (Media Cybernetics, 1997) in combination with a dissecting microscope equipped with a charged coupled device (CCD) camera (model: Toshiba IK-630) and a Pentium II computer equipped with a 640 × 480 pixel frame grab card and a 800 × 600 pixel monitor. The images were measured in microns after distance calibrations were incorporated. The distances from the focus to the distal edge of the section (ray radius) and from the focus to the distal edge of each growth band (annulus) were measured and recorded (Fig. 4). The focus, the growth band, and the false growth band (multiple bands) were defined according to Berkeley and Houde (1983), Tserpes and Tsimenides (1995), and Ehrhardt et al. (1996).

The marginal increment ratio (MIR), which was used to validate the reading of annuli, was estimated for each specimen by the following formula (Prince et al., 1988; Esteves et al., 1995):

$$MIR = (S - S_n)/(S_n - S_{n\ 1}),$$

where S = ray radius; and
S_n and $S_{n\ 1}$ = the distance from ray focus to bands n and $n-1$, respectively.

The mean MIR and the standard deviation were computed for each month by sex for all ages combined and also for each age separately.

Growth was analyzed by using the back-calculation of length-at-age for each sex. For this purpose, a relationship was determined between the ray radius and the LJFL. This relationship and the distance from the focus

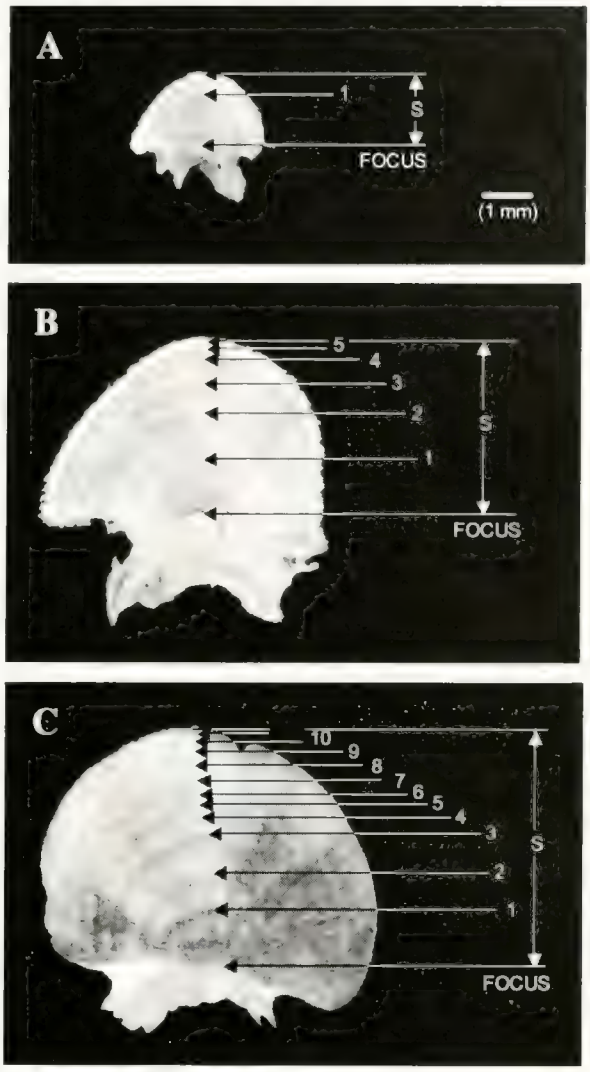

Figure 4

The section of three typical second anal fin rays of swordfish. Ray radius (S) measured from focus to edge; annuli for estimated age 1+ (**A**), age 5+ (**B**) and age 11+ (**C**).

to successive rings were used to back-calculate lengths at presumed previous ages (Ehrhardt, et al., 1996). For the relationship between ray radius and LJFL and the back-calculation of lengths-at-age, the following two methods were used.

Method I

The relationship between ray radius (S) and LJFL (L) was determined by using the standard linear regression procedure, $L = a + bS$ (Berkeley and Houde, 1983). This relationship and the distance from focus to successive growth bands, which we assumed to be based on annual growth events, were used to back-calculate the lengths at presumed ages by the following formula (Fraser, 1916):

$$L_n = a + \frac{S_n}{S}(L - a),$$

where L = LJFL at time of capture;
L_n = LJFL when band n was formed;
a = the intercept on the length axis from the regression line of length (L) on ray radius (S), e.g. $L = a + bS$; and
S_n = the distance from ray focus to band n.

Method II

The relationship between ray radius and LJFL was determined by using a power function procedure, $L = aS^b$ (Ehrhardt, 1992; Ehrhardt et. al., 1996). Parameters of this function were estimated by nonlinear least square fits to the observed data. This relationship and the distance from focus to successive growth bands were used to back-calculate the lengths at presumed ages by the following formula (Tserpes and Tsimenides, 1995; Ehrhardt et al., 1996):

$$L_n = \left(\frac{S_n}{S}\right)^b L,$$

where b = the exponent of the regression of length (L) on ray radius (S) which is assumed to be a power function of the form $L = a\,S^b$.

The data of the back-calculated length-at-age from method I and method II were then applied to the following standard von Bertalanffy growth equation (standard VB) and to the generalized growth function (generalized VB) (Richards, 1959):

Standard VB:

$$L_t = L_\infty\left(1 - e^{-k(t - t_0)}\right);$$

Generalized VB:

$$L_t = L_\infty\left(1 - e^{-K(1 - mt - t_0)}\right)^{1/m},$$

where L_t = the mean LJFL at age t;
L_∞ = the asymptotic length;
t_0 = the hypothetical age at length zero;
k and K = the growth coefficients; and
m = the fitted fourth growth-function parameter.

Parameters of the above two equations for male and female were estimated, respectively, by fitting a curve to the observed back-calculated LJFL-at-age by using a nonlinear least square procedure (Gauss-Newton method, NLIN of SAS Institute, 1990). The measure of goodness-of-fit chosen was r^2. A multivariate statistical procedure (Hotelling's T^2) was used to test for differences in growth between males and females (Bernard, 1981) for the two growth models and two methods. The r^2 values were ranked between the two different growth functions with the smaller as 1. A non-parametric test (Friedman 1937, 1940) was then employed

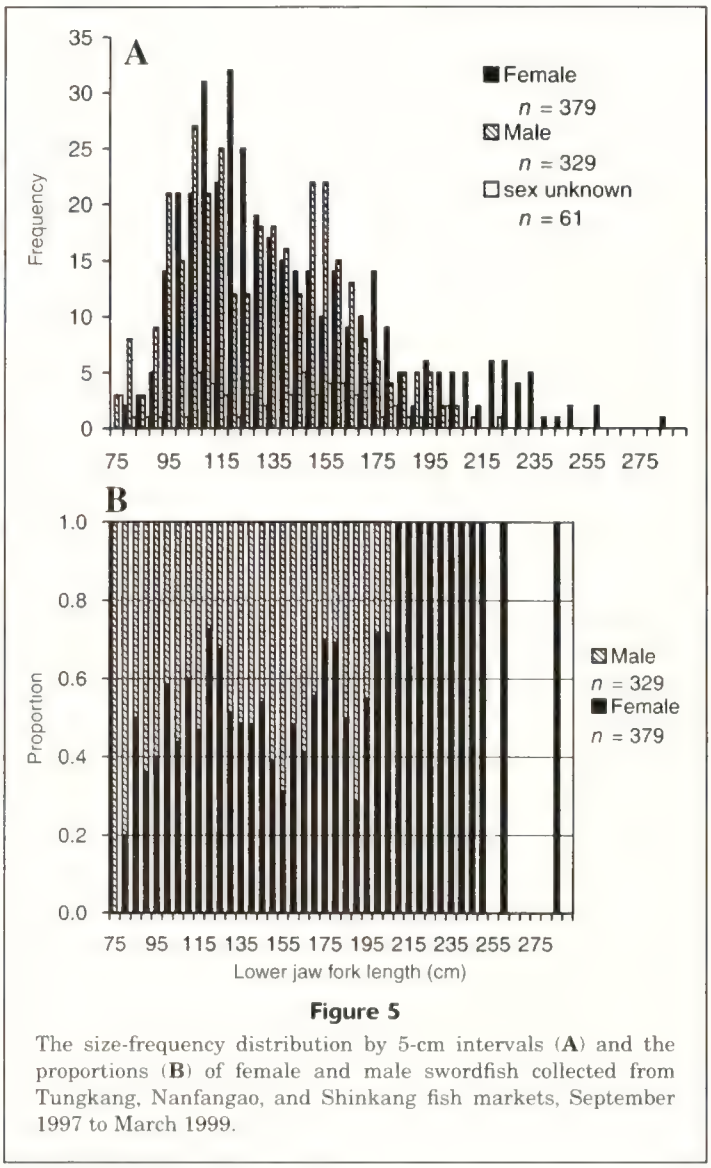

Figure 5

The size-frequency distribution by 5-cm intervals (**A**) and the proportions (**B**) of female and male swordfish collected from Tungkang, Nanfangao, and Shinkang fish markets, September 1997 to March 1999.

on the ranked results of r^2 to test the significance of the goodness-of-fit comparisons between the two growth functions (Chen et al., 1992). Friedman's test statistic χ^2_r was calculated with a correction for tied ranks (Zar, 1999). The association of rank ordering of r^2 values between the two growth functions was measured nonparametrically by using the Kendall coefficient of concordance (Kendall, 1962).

Results

Of the 685 anal fin rays sampled, 627 (334 females and 293 males) were aged successfully. The average percent error (APE) was 5.18% (5.09% for females and 5.29% for males) and the coefficient of variation (CV) was 8.50% (8.28% for female and 8.76% for males). The LJFL of the aged fish ranged from 83.4 to 246.6 cm for the females and from 83.3 to 206 cm for the males. The remaining 58 fin rays were considered unreadable mostly because the opaque-translution zonation was so unclear that annuli could not be defined (32 specimens); 7 specimens were unreadable because of the existence of multiple bands, which made the identification of annuli difficult or resulted in aging discrepancies between readings and readers; and 19 specimens were unreadable because of both the above factors.

For all the 769 swordfish with LJFL measured, individuals ranged from 83.4 to 290 cm for females and 78 to 206.6 cm for males (Fig. 5A). The proportion of the females (Fig. 5B) varied at sizes less than 195 cm, then increased to 100% at 210 cm and thereafter.

The relationship between LJFL and round weight for 227 specimens (sexes pooled) is shown in Figure 6; ANCOVA revealed no differences between males and females (P>0.05). The LJFL-EFL (eye fork length) conversion equation is $LJFL = 1.0647EFL + 7.7911$, with df = 563 and r^2=0.99.

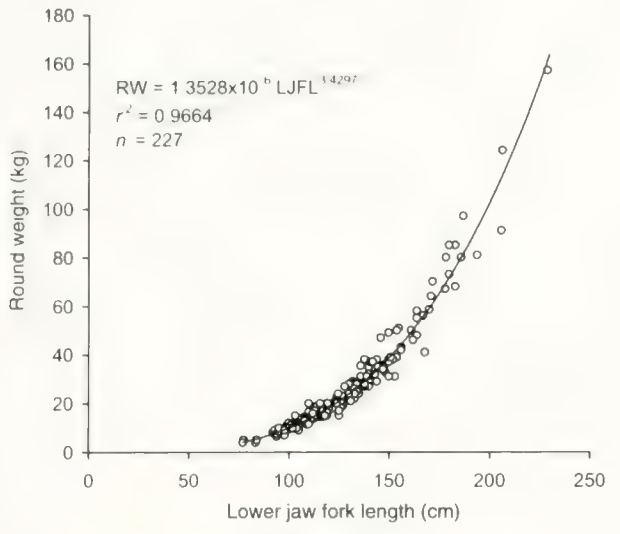

Figure 6

Relationship between round weight and lower jaw fork length for the swordfish collected from Shinkang fish market regardless of sex.

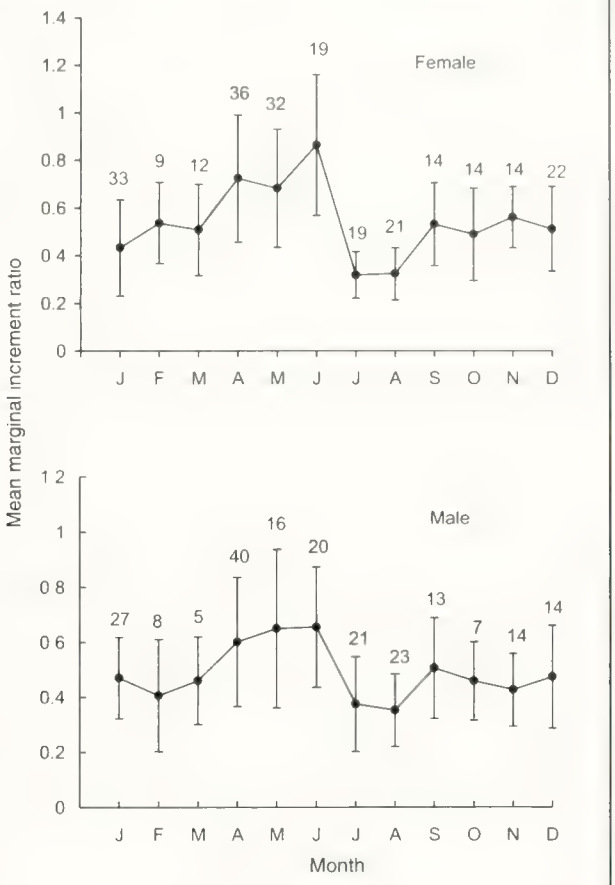

Figure 7

Monthly means of marginal increment ratio of female and male swordfish in the waters around Taiwan for all ages combined. Vertical bars are 1 SE, numbers on the top of vertical bars are sample sizes.

The monthly means of marginal increment ratio, MIR, for females with all ages combined, dropped drastically from the maximum of 0.86 in June to the minimum of 0.32 in July and August (Fig. 7). Similarly, the monthly means of MIR value for males declined sharply from the maximum of 0.65 in June to 0.37 and 0.35 in July and August. For both females and males, the monthly means of MIR during the period from September to March were not different (ANOVA, $P_{♀}$=0.95, $P_{♂}$=0.48), but the monthly means of MIR in April, May, and June were significantly higher than that in July or August, respectively (two sample t-tests, P<0.001). Also, the mean MIR in August was significantly lower than that in September (t-tests, $P_{♀}$<0.001, $P_{♂}$<0.01). The trends exhibited by monthly means of MIR for females and males for ages 2 to 5, respectively, were the same as those just described for all ages combined (Fig. 8). These patterns indicated the formation of one ring per year during the period from July to August. The MIR analysis by age was not performed for age 1 and ages greater than 5 because the formula used to determine MIR does not apply to samples less than or equal to age 1 and there was a lack of a sufficient number of samples for ages greater than 5.

The mean band radii, by band group for female and male, are shown in Table 1. The observed LJFLs of female and male swordfish were plotted against their corresponding ray radii for method I and method II, respectively (Fig. 9). The relationships between LJFL and ray radius are described as follows:

Method I Female: $LJFL = 21.137S + 65.091$ [r^2=0.8894, n=334];

Male: $LJFL = 19.966S + 68.160$ [r^2=0.8737, n=293].

Method II Female: $LJFL = 73.754S^{0.5193}$ [r^2 = 0.8753, n=334];

Male: $LJFL = 77.075S^{0.4772}$ [r^2=0.8742, n=293].

ANCOVA revealed significant differences in the relationship between the males and females for both methods (for method I, $F_{333, 292}$=8.36, P<0.001; for method II, $F_{333, 292}$=15.59, P=0.004). The average back-calculated lengths-at-age obtained using method I and method II are shown in Table 2. Growth rates were higher during the first year of age (mean 95.2 cm and 96.1 cm LJFL for males and females, respectively, for method I, compared to 88.6 cm and 90.4 cm LJFL for males and females, respectively, for method II). After the first year of age, the growth rates of both sexes slowed appreciably. Growth rates of females were always higher than those of males, especially after the age of three. Also, the growth rates were always higher for method II than for method I except for the first year of age. Fitted standard VB and generalized VB growth

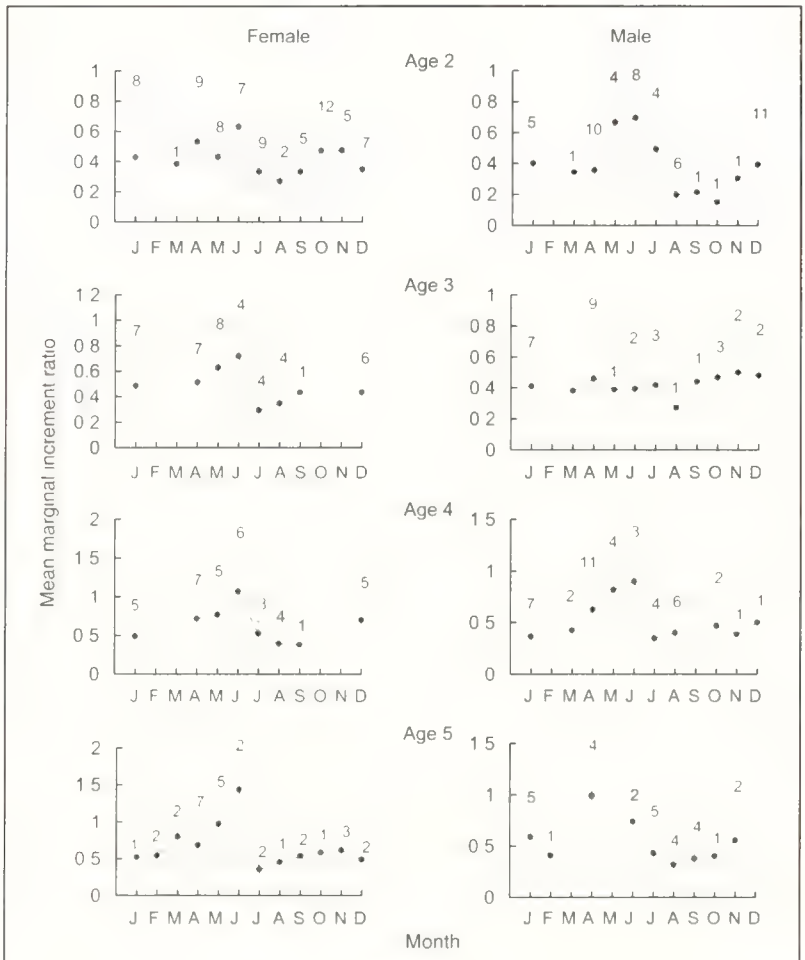

Figure 8

Monthly means of marginal increment ratio of female and male swordfish in the waters around Taiwan for ages 2 to 5 respectively. Vertical bars are 1 SE, numbers on the top of vertical bars are sample sizes.

curves for males and females with method I and method II back-calculation are shown in Figure 9, and the estimated parameters corresponding to each curve are shown in Table 3.

Hotelling's T^2 test results showed significant difference in growth parameters between female and male swordfish for either standard or generalized VB with either method I or method II back-calculation (Table 4). The calculated T^2 is considerably higher than the tabulated value in Table 4 for each case, and all the parameters, except for m of the generalized VB, significantly affect the differences in growth between male and female swordfish (The Roy-Bose simultaneous confidence intervals around differences between parameter values fail to include zero). The results of goodness-of-fit comparison showed that the generalized VB had larger r^2 ranks for method II, but had equal ranks with the standard VB for method I. Considering the tie rank groups in each sex-by-method, Friedman's χ^2_r statistics is 2 (n=4). This was not significant at the 5% level (i.e. χ^2=3.841, df=1), which indicated no significant difference in the r^2 rank ordering of the values between the two growth functions. Kendall's coefficient of concordance was 0.5 (n=4), which did not indicate a good agreement in the r^2 ranks for all sexes-by-method.

Discussion

Just as reported by Berkeley and Houde (1983), Radtke and Hurley (1983), Wilson and Dean (1983), Tsimenides and Tserpes (1989), Ehrhardt (1992), Tserpes and Tsimenides (1995), and Stone and Porter (1997), females in our study were typically larger than males although the length-weight relationship between the sexes did not differ significantly. The overall sex ratio for the sampling period in our study did not deviate significantly from 1:1 (P<0.01) but differed substantially from the ratios of 2.3 females to 1 male and 2.7 females to 1 male reported respectively by Stone and Porter (1997) and Caton et al. (1998). This discrepancy may have been caused by the dif-

Table 1

Mean radius from focus to distal edge of each band of female (**A**) and male (**B**) swordfish in the waters around Taiwan. Roman numerals indicate the number of bands.

A

Band class	Sample size	Mean radius (mm) from focus to each band											
		I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
0	2												
1	86	1.44											
2	76	1.44	2.38										
3	42	1.44	2.43	3.09									
4	39	1.51	2.34	3.08	3.52								
5	26	1.43	2.39	3.26	3.84	4.23							
6	20	1.51	2.35	3.14	3.77	4.24	4.75						
7	13	1.43	2.40	3.33	3.90	4.40	4.80	5.20					
8	13	1.58	2.60	3.47	4.10	4.52	4.95	5.39	5.84				
9	7	1.60	2.36	3.18	3.81	4.35	4.86	5.39	5.80	6.26			
10	2	1.49	2.37	3.35	3.96	4.46	4.84	5.33	5.64	6.21	6.66		
11	3	1.55	2.43	3.23	3.81	4.18	4.67	5.23	5.76	6.25	6.65	6.80	
12	5	1.50	2.44	3.30	3.88	4.41	5.02	5.39	5.94	6.29	6.69	6.98	7.24
Mean		1.49	2.41	3.24	3.84	4.35	4.84	5.32	5.80	6.25	6.66	6.89	7.24
SD		0.18	0.23	0.34	0.40	0.40	0.49	0.40	0.42	0.33	0.46	0.57	0.40
Growth increase			0.91	0.84	0.60	0.50	0.49	0.48	0.47	0.46	0.41	0.22	0.35

B

Band class	Sample size	Mean radius (mm) from focus to each band									
		I	II	III	IV	V	VI	VII	VIII	IX	X
0	2										
1	84	1.47									
2	57	1.32	2.16								
3	32	1.28	2.36	3.06							
4	43	1.31	2.32	3.04	3.51						
5	27	1.32	2.32	3.11	3.65	4.05					
6	22	1.32	2.44	3.21	3.71	4.11	4.47				
7	9	1.39	2.41	3.21	3.75	4.28	4.62	4.98			
8	8	1.33	2.52	3.24	3.82	4.26	4.66	5.02	5.37		
9	4	1.25	2.25	3.35	3.92	4.29	4.70	5.05	5.37	5.74	
10	5	1.40	2.36	3.16	3.93	4.41	4.80	5.11	5.47	5.76	6.06
Mean		1.34	2.35	3.17	3.76	4.23	4.65	5.04	5.40	5.75	6.06
SD		0.17	0.22	0.26	0.30	0.31	0.33	0.32	0.35	0.39	0.38
Growth increase			1.01	0.82	0.58	0.48	0.41	0.39	0.36	0.35	0.20

ference in size ranges of LJFL sampled for studying the sex ratio (Mejuto, et al., 1995). Most of the LJFL in our sample ranged between 100 and 185 cm, close to Arocha and Lee's (1995) middle size range within which the sex ratio was also almost 1:1 (Arocha and Lee, 1995). Besides the size range difference, the differences in geographical areas and seasons can also affect the sex ratio (Hoey, 1991; Mejuto et al., 1991). The proportion of females in our study, which increased to 100% at 210 cm and thereafter, was similar to those described by Turner et al. (1996), Stone and Porter (1997), and DeMartini et al. (2000).

Several genetic studies (Grijalva-Chon et al., 1994; Rosel and Block, 1996; Chow et al., 1997; Chow, 1998) have been unable to reject the hypothesis that swordfish comprise a single, homogenous population in the Pacific. However, from recent analyses of mtDNA, Reeb et al. (2000) concluded that swordfish are not homogenous in the Pacific. They found significantly different northern and southern populations in the western Pacific and several overlapping swordfish populations may occur in the eastern Pacific, making swordfish genetically continuous there. Gene flow between the populations occurs through

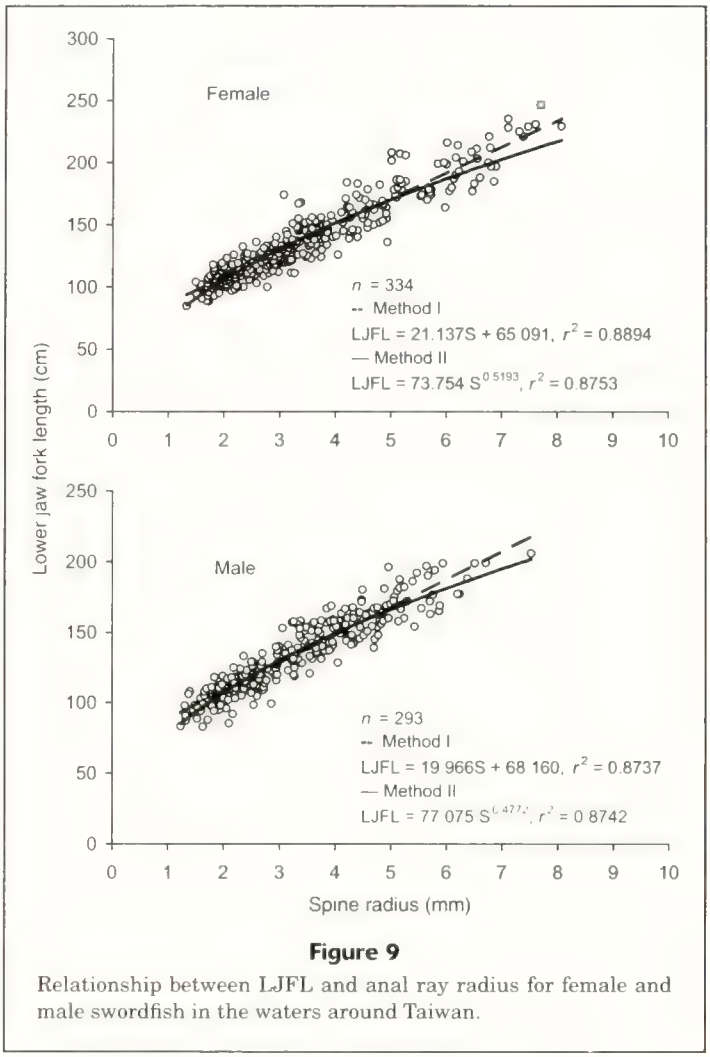

Figure 9

Relationship between LJFL and anal ray radius for female and male swordfish in the waters around Taiwan.

a horseshoe-shaped corridor, running between the northwestern Pacific, across to the eastern Pacific and back to the southwestern Pacific (Ward and Elscot, 2000). According to Reed's studies, the swordfish in our samples can be considered a part of the northern population in the western Pacific Ocean.

We found that anal-fin rays are useful for aging swordfish; they are easily sampled without reducing the economic value of the fish and can be read easily (the growth rings stand out clearly). This aging tool is especially important because swordfish lack scales and their very small otoliths are not amenable to traditional aging techniques (Ovchinnikov, 1971; Beckett, 1974; Tserpes and Tsimenides, 1995). Moreover, fin rays can be easily stored for future reexamination (Compeán-Jimenez and Bard, 1983). One problem associated with the fin-ray method used in our study, also indicated by Berkeley and Houde (1983) and Tserpes and Tsimenides (1995), was the possible existence of multiple bands and the missing first annulus in larger fish. However, González-Garcés and Fariña-Perez (1983) and Tserpes and Tsimenides (1995) noted that experienced readers could overcome the prob-

Table 2

Mean back-calculated lower jaw fork lengths at age for swordfish in the waters around Taiwan.

	Back-calculated length (cm)			
	Method I		Method II	
Age (yr)	Male	Female	Male	Female
1	95.19	96.07	88.60	90.35
2	114.86	115.70	114.96	116.18
3	131.88	133.41	133.80	136.47
4	143.12	146.30	145.22	150.35
5	152.14	157.99	154.40	162.91
6	159.15	169.95	161.36	175.34
7	165.60	180.48	167.84	186.40
8	174.76	190.14	176.87	195.83
9	184.00	198.40	185.23	204.62
10	190.89	207.79	191.58	214.15
11		215.06		220.58
12		222.15		226.62

Table 3

Parameter estimates for the standard von Bertalanffy and the generalized von Bertalanffy growth models for swordfish in the waters around Taiwan. Numbers in parentheses are standard errors.

	Standard von Bertalanffy growth model				Generalized von Bertalanffy growth model			
	Method I		Method II		Method I		Method II	
Parameter	Male	Female	Male	Female	Male	Female	Male	Female
L_∞	224.170 (12.802)	281.809 (6.805)	207.520 (8.465)	267.441 (6.517)	231.772 (26.937)	301.877 (11.068)	213.052 (19.153)	300.656 (38.869)
k	0.140 (0.025)	0.101 (0.006)	0.198 (0.031)	0.130 (0.009)				
K					0.066 (0.103)	0.060 (0.055)	0.086 (0.035)	0.040 (0.116)
t_0	–3.089 (0.523)	–3.204 (0.171)	–1.955 (0.406)	–2.302 (0.190)	–1.556 (2.942)	–2.036 (1.263)	–0.626 (1.196)	–0.750 (2.272)
m					–0.625 (2.388)	–0.409 (0.943)	–0.768 (1.730)	–0.785 (1.324)

Table 4

Results of the multivariate (Hotelling's T^2) tests for difference between the estimated von Bertalanffy growth parameters of female and male swordfish in the waters around Taiwan.

	Standard von Bertalanffy growth model		Generalized von Bertalanffy growth model	
	Method I	Method II	Method I	Method II
T^2	20715.1	56005.2	1614630	6782.34
df	3, 623	3, 623	4, 623	4,623
$T^2_{0.01,df}$	11.48	11.48	13.46	13.46
99% CI for[1]				
$L_\infty - L_{\infty,f}$	53.842 ~ 61.436**	56.452 ~ 63.390**	68.845 ~ 71.365**	85.621 ~ 89.587**
$k - k_f$	–0.044 ~ –0.034**	–0.071 ~ –0.065**		
$K - K_f$			–0.008 ~ –0.004**	–0.050 ~ –0.042**
$t_0 - t_{0,f}$	–0.216 ~ –0.014**	–0.406 ~ –0.288**	–0.542 ~ –0.418**	–0.163 ~ –0.085**
$m - m_f$			0.205 ~ 0.227**	–0.062 ~ 0.028

[1] Roy-Bose simultaneous confidence intervals around differences between parameter values.

** Indicates the parameter tested that significantly affects differences in growth between the females and the males at a significant level of 0.01.

lem of multiple bands by determining whether the bands were continuous around the circumference of the entire ray section and by judging their distance from preceding and following bands. In our study, 91 out of the 627 readable specimens had "multiple bands" that were read without a problem by using these criteria. Of the 26 discarded specimens that had multiple unreadable bands, most were found in swordfish larger than 200 cm in size. The missing first band in larger fish can be estimated from observations of its position on young specimens where the first band is visible. Similar approaches for solving the problem of missing band have also been used for Atlantic swordfish (Berkeley and Houde, 1983) and eastern Mediterranean swordfish (Tserpes and Tsimenides, 1995).

Results of marginal increment ratio analysis (Figs. 7 and 8) suggest one growth ring (annulus) is formed each year from July to August, which is toward the end of the spawning period for the swordfish in the north Pacific (Yabe et al., 1959). Although the timing of annulus deposition coincides with the swordfish's spawning season in the north Pacific, it may also be related to swordfish migration, as suggested by Berkeley and Houde (1983) for Atlantic

swordfish and by Tserpe and Tsimenides (1995) for eastern Mediterranean swordfish. The relationship between annulus formation and migration for the western Pacific swordfish should be investigated. Others (Nelson and Manooch, 1982; Beckman et al., 1990; Sturm and Salter, 1990; Ferreira and Russ, 1994; Franks et al., 1999) have commented on the physiological nature of annulus formation and the importance of environmental factors, suggesting that reproduction may not be the sole determining factor in annulus deposition. Our results only partially validated age. Validation of ages requires either a mark-recapture study or the identification of known-age fish in the population (Beamish and McFarlane, 1983; Prince et al., 1995; Tserpes and Tsimenides, 1995; Sun et al., 2001).

According to Hotelling's T^2 analysis, the female and male swordfish in either method I or method II of both standard VB and generalized VB grew differently. Those of the generalized VB had a little larger r^2 ranks than those of the standard VB, although the goodness-of-fit of nonparametric analysis of r^2 ranks did not show a significant difference between two growth equations (P=0.22). In addition, the generalized VB appeared to fit the data well over the range of ages and it provided more realistic growth patterns for juveniles less than one year. However, the standard VB, commonly used to describe fish asymptotic growth, did not fit these data well, and generated grossly overestimated values for individuals less than one year (Table 3 and Fig. 10) (Ehrhardt, 1992; Ehrhardt et al., 1996).

In Table 3, the t_0 values estimated for the generalized VB with method II (i.e. a power function was used to describe the relationship between ray radius and LJFL) were much closer to zero than those estimated for the generalized VB with method I (i.e. a simple linear function was used to describe the relationship between ray radius and LJFL). Also, Ehrhardt (1992), Ehrhardt et al. (1996), and Tserpes and Tsimenides (1995) favored the power function (method II) because they believed its description to be more biologically realistic. Therefore, the parameter estimates for the generalized VB model with method II shown in Table 3 are recommended as the most acceptable for determining the age composition of swordfish in the waters around Taiwan.

Age-length relationships of swordfish (Fig. 11) are mostly based on Atlantic specimens (Berkeley and Houde, 1983; Radtke and Hurley, 1983; Wilson and Dean, 1983; Ehrhardt, 1992; Ehrhardt et al., 1996), and a few on Pacific samples (Yabe et al., 1959; Castro-Longoria and Sosa-Nishizaki, 1998; Uchiyama et al., 1998; Castro-Longoria[1]; Uchiyama[2]). Differences in estimates of growth parameters for males and females arise from the use of different hard parts, e.g. anal-fin rays (our study) versus otoliths (Radtke and Hurley, 1983; Wilson and Dean, 1983) or vertebrae (Esteves et al., 1995), artifacts of preparation, or interpretation. Even though we used the same method as Ehrhardt (1992), Tserpes and Tsimenides (1995), and Ehrhardt et al. (1996), observed difference could be related to geographical coverage of the studies. Our results were in the mid-range of previous estimates, well within the range of variation that might be expected due to the somewhat subjective nature of the processing, measuring, and interpreting of growth rings on fin rays. Therefore, we believe our growth parameter estimates are appropriate for use in assessment studies of the northern swordfish population in the western Pacific Ocean.

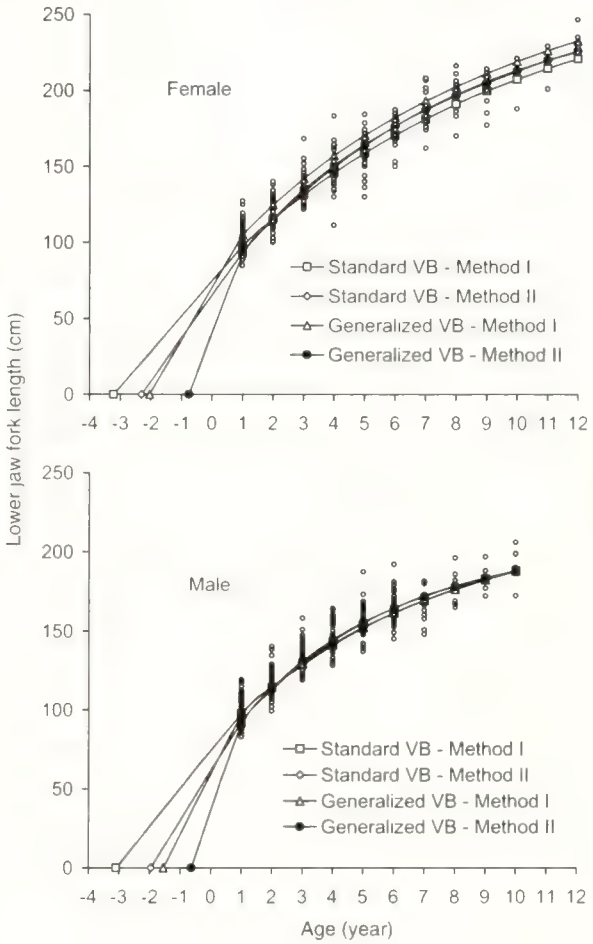

Figure 10

Standard and generalized von Bertalanffy growth curves for female and male swordfish in the waters around Taiwan.

Acknowledgments

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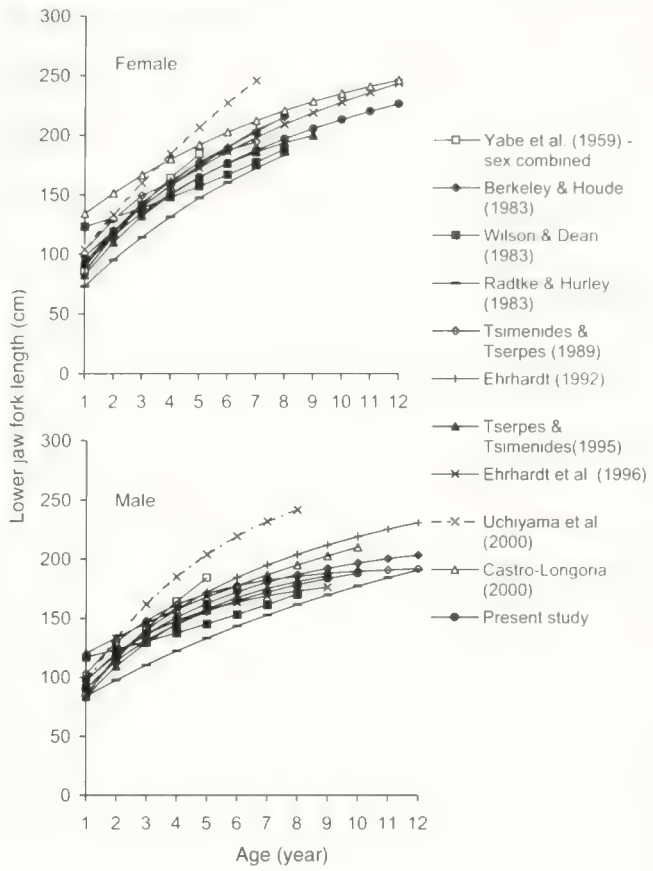

Figure 11

A comparison of the growth curves of female and male swordfish estimated by different authors.

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Distribution and co-occurrence of rockfishes (family: Sebastidae) over trawlable shelf and slope habitats of California and southern Oregon

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Abstract—The rockfishes of the sebastid genus *Sebastes* are a very important fishery resource off the coasts of California and southern Oregon. However, many of the 54 managed stocks of west coast rockfish have recently reached historically low population levels, leading fishery managers to reexamine current management practices. Management of rockfish stocks as multispecies aggregates, as opposed to independent stocks within the groundfish fishery, can be more desirable when nontargeted bycatch, discard, and management complexity are considered. Rockfish assemblage structure and species co-occurrences were determined by using data from the Alaska Fisheries Science Center triennial continental shelf bottom trawl survey. The weight of rockfish species in trawl catches was expressed as a catch-per-unit-of-effort (CPUE) statistic, from which species spatial distributions, overlaps, diversity, and richness were analyzed. Multidimensional scaling of transformed CPUE data was employed in indirect gradient and multivariate partitioning analyses to quantify assemblage relationships. Results indicated that rockfish distributions closely match the bathymetry of coastal waters. Indirect gradient analysis suggested that depth and latitude are the principal factors in structuring the spatial distributions of rockfish on trawlable habitat. In addition, four assemblages were identified through the joint evaluation of species' distributions and multivariate partitioning analyses: 1) deep-water slope; 2) northern shelf; 3) southern shelf; and 4) nearshore. The slope, shelf, and nearshore groups are found in depth ranges of 200–500 m, 100–250 m, and 50–150 m, respectively. The division of northern and southern shelf assemblages occurs over a broad area between Cape Mendocino and Monterey Canyon. The results of this analysis are likely to have direct application in the management of rockfish stocks off the coasts of southern Oregon and California.

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Rockfishes (family Sebastidae according to recent work by Eschmeyer (1998) and Kendall (2000), genera *Sebastes* and *Sebastolobus*) are a very important part of the groundfish fishery off the United States west coast, representing a relatively high value in the market. In 1997, rockfish species accounted for 17% of total west coast groundfish landings, but 33% of total exvessel value (Herrick et al.[1]). Rockfishes on the U. S. west coast are managed under the groundfish Fishery Management Plan (FMP) by the Pacific Fishery Management Council. Some of the 52 *Sebastes* and 2 *Sebastolobus* species that are included in the FMP are managed as single-species stocks, and other, generally less well-known species, are managed as part of larger multispecies aggregations. Moreover, the 54 "rockfishes" listed in the FMP do not include all of the *Sebastes* spp. found in the region. More than 70 species are known from the northeast Pacific Ocean (Eschmeyer et al., 1983; Chen, 1986).

The current status of the principal west coast rockfish stocks is that many have reached historically low levels and the population sizes of many of the minor species remain virtually unknown. Moreover, seven rockfishes (bocaccio (*S. paucispinis*), cowcod (*S. levis*), canary (*S. pinniger*) darkblotched (*S. crameri*), widow (*S. entomelas*), and yelloweye (*S. ruberrimus*) rockfishes, and Pacific ocean perch (*S. alutus*) have recently been declared overfished by the National Marine Fisheries Service. The continuing declines in rockfish populations and other groundfish stocks off the U. S. west coast have prompted changes in harvest policy and other management practices (Ralston, 1998, 2002).

Management of exploited fish stocks on an individual basis often results in discarded bycatch of nontargeted species, which is wasteful. In contrast, management of species as aggregates or complexes can be more practical and desirable (Ralston and Polovina, 1982; Leaman and Nagtegaal, 1986; Fujita et al., 1998). However, the multispecies management approach is only as good as the assemblage or group definitions used, which depend on the availability and accuracy of species-specific distributional information. Most fisheries managers rely on fishery-independent surveys or at-sea observations of fishery catches recorded in vessel logbooks or noted by observers to provide spatial information on fish abundance patterns. Data collection for groundfish population assessments off the coast

[1] Herrick, S. F., J. Hastie, and W. Jacobson. 1998. Economic status of the Washington, Oregon, and California groundfish fisheries. *In* Pacific Fishery Management Council, Status of the Pacific Coast groundfish fishery through 1998 and recommended biological catches for 1999: stock assessment and fishery evaluation. Pacific Fishery Management Council, 2130 SW Fifth Ave., Suite 224, Portland, Oregon 97201.

of California consists primarily of sampling commercial and recreational landings at ports, and for these landings there is little information on catch location (Pearson and Erwin, 1997; Sampson and Crone, 1997). The National Marine Fisheries Service, Alaska Fisheries Science Center (AFSC) westcoast triennial continental shelf bottom-trawl survey, which enters into California waters, has yielded useful spatial information for determining groundfish distributions and co-occurrences. This survey began in 1977 as a rockfish survey but changed focus in subsequent years, depending on the particular information needs at the time (Dark and Wilkins, 1994; Wilkins et al., 1998). For the eight surveys conducted from 1977 to 1998, the shelf trawl survey covered the area from central Vancouver Island, British Columbia, to Point Conception, California, at depths ranging from 50 to 500 m (Wilkins et al., 1998).

Along the U.S. west coast, 60–65% of the groundfish catch (exclusive of Pacific whiting) is taken off the coasts of Washington and Oregon (PFMC[2]). This area has been the focus of past studies examining groundfish population distributions and assemblages (e.g. Gabriel and Tyler, 1980; Leaman and Nagtegaal, 1986; Rickey and Lai, 1990; Rogers and Pikitch, 1992; Weinberg, 1994; Jay, 1996; Gunderson, 1997). In these previous studies of rockfish distributions and groupings, rockfish could be broken into shelf and slope assemblages (e.g. Rogers and Pikitch, 1992; Weinberg, 1994). These studies have all indicated that along the Oregon–Washington coast a "slope" or deep-water rockfish assemblage exists, consisting of darkblotched rockfish, Pacific ocean perch, splitnose rockfish (*S. diploproa*), yellowmouth rockfish (*S. reedi*), and shortspine thornyhead (*Sebastolobus alascanus*). In addition, a "shelf" or bottom rockfish assemblage consists of yellowtail rockfish (*S. flavidus*), canary rockfish (*S. pinniger*), sharpchin rockfish (*S. zacentrus*), greenstriped rockfish (*S. elongatus*), rosethorn rockfish (*S. helvomaculatus*), and redstripe rockfish (*S. proriger*). Weinberg (1994) also examined patterns in abundance and number of rockfish species with respect to depth gradients. Both abundance and the number of species increased with depth to a maximum in the range of 151–250 m but both quantities decreased at depths greater than 250 m.

Groundfish assemblages off California have not been studied, primarily because of the absence of detailed at-sea fishery data collection programs and because of smaller landings. Although California landings account for only 35% of the nonwhiting groundfish total (PFMC[2]), nearly 43% of west coast rockfish landings are taken in California waters (Herrick et al.[1]). Thus, an understanding of the distribution and co-occurrence of rockfishes off the California coast would help with efforts to implement effective fishery management actions leading to a sustainable California rockfish fishery. In particular, an understanding of rockfish distributions and co-occurrences could lead to improved definitions of species complexes. Weinberg (1994) analyzed rockfish assemblages of the "Columbia" and U.S. portion of the "Vancouver" fishery management areas, as specified by the International North Pacific Fisheries Commission (INPFC) (Fig. 1). In part to complement Weinberg's (1994) analysis, we analyzed the AFSC continental shelf trawl survey data from the more southerly waters of the Eureka, Monterey, and Conception INPFC areas, i.e. all sampling conducted south of lat. 43°N (Fig. 1).

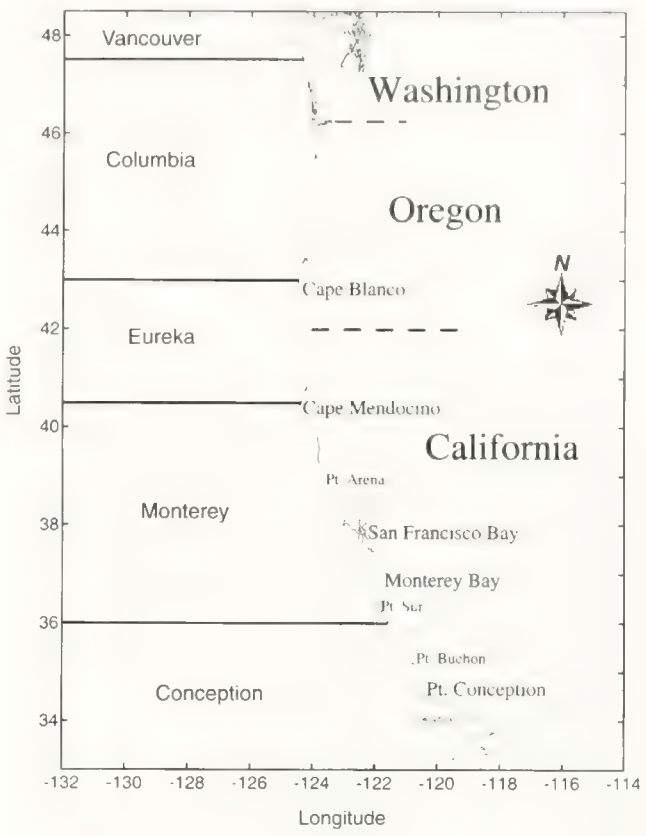

Figure 1

Map of the west coast of the United States, including names of important coastal features and International North Pacific Fisheries Commission management areas.

Materials and methods

Rockfish likely form aggregations or complexes as a response to oceanographic and bathymetric features. For this reason the bathymetry of the region encompassed by the limits of the survey area in the Eureka, Monterey, and Conception INPFC areas was characterized. The study area is the area of marine waters located from lat. 34° to 43°N within a depth range of 50–500 m. Bathymetric data for this region were obtained from the National Ocean Service Hydrographic Data Base (NOSHDB). The

[2] PFMC (Pacific Fishery Management Council). 2000. Status of the Pacific Coast groundfish fishery through 2000 and recommended acceptable biological catches for 2001—stock assessment and fishery evaluation. Pacific Fishery Management Council, 2130 SW Fifth Ave., Suite 224, Portland, Oregon 97201.

NOSHDB contains data digitized from hydrographic surveys completed from 1930 to 1965 and from survey data acquired digitally on NOS survey vessels since 1965. The total amount of habitat by depth and latitude, as well as the location of the shelf break, was determined by analysis of the NOSHDB.

Because the NOSHDB contains a vast amount of data, we computed depth profiles only at each 0.5 interval of latitude. Profiles were obtained by contouring a narrow (0.05°=5.56 km) swath of depth soundings by using inverse distance to a power for interpolations (Surfer, 1995). After correcting for latitudinal differences in the relationship between longitude and distance, the resulting depth profiles were used to estimate the total amount of habitat [km] in 50-m depth intervals. In addition, the distance offshore and the depth of the continental shelf break were estimated. The location of the shelf break was estimated by using a three-parameter segmented linear model that minimized the sums of squared differences between a contoured depth profile and points along two linear sections of a segmented line. The fitted join point of the two segments was then used to estimate the location of the shelf break. In the estimation procedure, the offshore end of the offshore segment was fixed at the exact 500 m depth value obtained from the computed profiles.

Information on rockfish abundance was obtained from trawl survey data collected by the Resource Assessment and Conservation Engineering division of the AFSC. Trawl samples were generally collected by using a sampling design that was stratified by depth and latitude, and where allocation of sample sizes was based on prior fishery catches (Wilkins et al., 1998). From 1977 to 1998, trawl samples in the Eureka, Monterey, and Conception INPFC areas (Fig. 1) were typically taken between 50 and 500 m from June to August with a standardized Nor'eastern high-opening rockfish bottom trawl rigged with roller gear. Measurements recorded for each trawl sample were the following: trawl net width and height; time of the tow; distance traveled; and the number and weight of species in the catch (Wilkins et al., 1998).

The fundamental objective of the AFSC triennial continental shelf trawl survey is to estimate the distribution and abundance of fishes vulnerable to capture by bottom trawl along the U. S. west coast. This basic goal has not changed since the first year of the survey in 1977, although specific objectives have changed over time, which has resulted in alterations in the distribution of sampling effort. For example, sampling effort in 1977 was stratified by depth and latitude according to rockfish fishery information. Sampling efforts in 1980, 1983, and 1986 were shifted to improve biomass estimates of canary and yellowtail rockfish. However, the lack of any significant improvement in the precision of the rockfish biomass estimates prompted a shift in the 1989 and 1992 surveys to include all demersal groundfish and to improve estimates of Pacific hake (*Merluccius productus*) and juvenile sablefish (*Anoplopoma fimbria*) abundance. More recently in 1995 and 1998 the survey was expanded to include slope rockfish found in deeper waters (to 500 m) with an emphasis on obtaining a uniform sampling density. These changes in the goals and objectives of the AFSC shelf survey significantly altered the data on the spatial distribution of samples over time, which, in turn, confounded interannual comparisons of the spatial distributions of rockfish species.

Due to changes in survey design detailed above, all years of the survey were simply pooled into a single composite data set, from which the starting position of each haul, depth of haul [m], net width (m), distance towed (km), numbers of species collected, and species weights (kg) were extracted for analysis. The distribution of all hauls was analyzed by depth and latitude to reveal any patterns that might affect inferences about rockfish distributions or co-occurrences. Because management is primarily concerned with biomass estimates of abundance, only species weights were used in our analysis. All trawl-specific species weight measurements were converted to a catch-per-unit-of-effort (CPUE) statistic by dividing species catch weight by the product of the distance towed and net width, i.e. the area swept (ha). An analysis of the frequency of occurrence of each species in trawls was conducted to obtain a subset of the most ubiquitous rockfishes for use in all subsequent analyses. These species were selected based on their occurrence in at least six of the eight survey years, with the exception of halfbanded rockfish (*S. semicinctus*), which was included because it yielded moderately frequent catches in five of eight years (Table 1).

The data representing the selected subset of species were plotted by depth and latitude to display distributional patterns of CPUE. Next, interspecific distributional overlaps were computed by calculating the percentage of joint occurrences with other species based on presence or absence (Krebs, 1989). Joint occurrences were determined both on a trawl-specific basis and after catches had been aggregated into 50-m depth and 0.5°-latitude intervals. In addition, *Sebastes* diversity and species richness were computed for each haul to summarize the overall distribution of rockfishes captured in the survey. For our analysis, diversity was computed by using the Shannon-Wiener index, and the number of species was used to scale richness (Krebs, 1989). Diversity and richness measures were then spatially contoured over depth and latitude dimensions to display spatial structure (Surfer, 1995).

Distributional patterns and groupings of rockfish based on the CPUE data were analyzed by indirect gradient analysis by using multivariate ordination and partitioning methods. Multivariate analyses are often strongly influenced by the choice of distance or (dis)similarity measure. Members of the set of Minkowski distance measures (e.g. Manhattan, Euclidean, maximum, etc.) tend to be strongly affected by extreme values. Moreover, species composition data from trawl surveys have a high proportion of zero catches and a distance measure that is little affected by this property is desirable. The Bray-Curtis index, also known as Czekanowski's quantitative index, is a commonly used statistic in other similar applications and is robust to the presence of zero values (see Bloom, 1981; Field et al., 1982; Krebs, 1989; Rogers and Pikitch, 1992; Weinberg, 1994; Meuter, 1999). A fourth-root transformation of the data was conducted before calculation of the Bray-Curtis index, as suggested by Field et al. (1982) and as implemented by

Table 1

Frequency of trawl samples with rockfish (family: Sebastidae) present in the Eureka, Monterey, and Conception areas from 1296 AFSC triennial shelf bottom trawl survey samples. The first 26 species (in bold) were included in the detailed analyses; the remaining 23 were not.

		Survey year								
Common name	Scientific name	1977	1980	1983	1986	1989	1992	1995	1998	Total
Stripetail rockfish	*Sebastes saxicola*	155	47	53	55	60	78	114	96	658
Chilipepper	*Sebastes goodei*	119	35	39	48	53	80	87	81	542
Splitnose rockfish	*Sebastes diploproa*	211	31	46	16	20	34	88	95	541
Shortspine thorneyhead	*Sebastolobus alascanus*	149	22	46	19	21	28	83	95	463
Greenstriped rockfish	*Sebastes elongatus*	58	23	56	57	44	57	72	75	442
Bocaccio	*Sebastes paucispinis*	127	65	46	53	40	30	41	26	428
Shortbelly rockfish	*Sebastes jordani*	101	38	20	56	45	59	62	42	423
Darkblotched rockfish	*Sebastes crameri*	122	31	56	28	36	38	56	51	418
Aurora rockfish	*Sebastes aurora*	83	1	2	1			56	60	203
Widow rockfish	*Sebastes entomelas*	42	23	26	10	14	28	30	28	201
Canary rockfish	*Sebastes pinniger*	31	21	39	22	17	17	17	34	198
Redbanded rockfish	*Sebastes babcocki*	51	12	20	8	12	17	37	21	178
Sharpchin rockfish	*Sebastes zacentrus*	8	13	15	14	16	32	22	23	143
Bank rockfish	*Sebastes rufus*	57	9	8	3	3	7	32	8	127
Yellowtail rockfish	*Sebastes flavidus*	17	10	26	14	8	18	19	10	122
Pacific ocean perch	*Sebastes alutus*	24	13	22	5	5	14	17	20	120
Blackgill rockfish	*Sebastes melanostomus*	49	1	3			1	30	35	119
Halfbanded rockfish	*Sebastes semicinctus*	6				13	40	31	27	117
Greenspotted rockfish	*Sebastes chlorostictus*	23	8	6	16	14	6	24	15	112
Cowcod	*Sebastes levis*	11	2	4	0	14	2	22	12	67
Rosethorn rockfish	*Sebastes helvomaculatus*	14	3	7	4	4	7	11	12	62
Brown rockfish	*Sebastes auriculatus*		3	5	7	6	3	4	1	29
Copper rockfish	*Sebastes caurinus*	2	1	5	2	6	4	5	4	29
Vermilion rockfish	*Sebastes miniatus*	2		1		6	7	3	1	20
Redstripe rockfish	*Sebastes proriger*			3	3	2	2	2	7	19
Yelloweye rockfish	*Sebastes ruberrimus*		2	2	3	5	3	1	1	17
Longspine thorneyhead	*Sebastolobus altivelis*	1						19	24	44
Rougheye rockfish	*Sebastes aleutianus*	7				1	1	7	12	28
Unidentified rockfish	*Sebastes* sp.	3		5	1	2	4	5	3	23
Flag rockfish	*Sebastes rubrivinctis*	20			1	1		1		23
Tiger rockfish	*Sebastes nigrocinctus*		2		10					12
Pygmy rockfish	*Sebastes wilsoni*			2	3	1	2	1	3	12
Squarespot rockfish	*Sebastes hopkinsi*					1	5	4	1	11
Greenblotched rockfish	*Sebastes rosenblatti*			1		2	4	1	3	11
Speckled rockfish	*Sebastes ovalis*	2	1		1	1	1		1	7
Shortraker rockfish	*Sebastes borealis*	2	1				1	1	2	7
Blue rockfish	*Sebastes mystinus*					1	1	2	1	5
Pink rockfish	*Sebastes eos*	2					1	1		4
Black rockfish	*Sebastes melanops*		1	1	1		1			4
Olive rockfish	*Sebastes serranoides*	1					2			3
Silvergray rockfish	*Sebastes brevispinis*				2					2
Yellowmouth rockfish	*Sebastes reedi*				2					2
California scorpionfish	*Scorpaena guttata*	1				1				2
Starry rockfish	*Sebastes constellatus*					1				1
Calico rockfish	*Sebastes dalli*					1				1
Freckled rockfish	*Sebastes lentiginosus*					1				1
Rosy rockfish	*Sebastes rosaceus*						1			1
Harlequin rockfish	*Sebastes variegatus*	1								1
Chameleon rockfish	*Sebastes phillipsi*	1								

Meuter (1999). A different measure of similarity, based on converting the data to presence-absence binary form and computing the proportion of nonzero values held in common, has also been used (Krebs, 1989). However, preliminary analyses indicated very little difference between the Bray-Curtis and binary similarity measures (r=0.973). Therefore, the Bray-Curtis similarity measure was used in all subsequent multivariate analyses.

Ordination techniques used in indirect gradient analysis were principal components, detrended correspondence analysis, and multidimensional scaling (Rogers and Pikitch, 1992; Mahon et al., 1998; Meuter, 1999). Multidimensional scaling (MDS) has the advantage of not requiring an assumption about the underlying response model and has been shown to be robust to different relationships of species abundances and environmental gradients (Minchin, 1987; Meuter, 1999). In our study we used MDS in conjunction with the Bray-Curtis similarity measure, similar to previous analyses (Field et al., 1982; Meuter, 1999). The first three dimensions from the MDS were extracted, plotted, and correlated with suspected gradients, which were then used to numerically define assemblage groupings in the data.

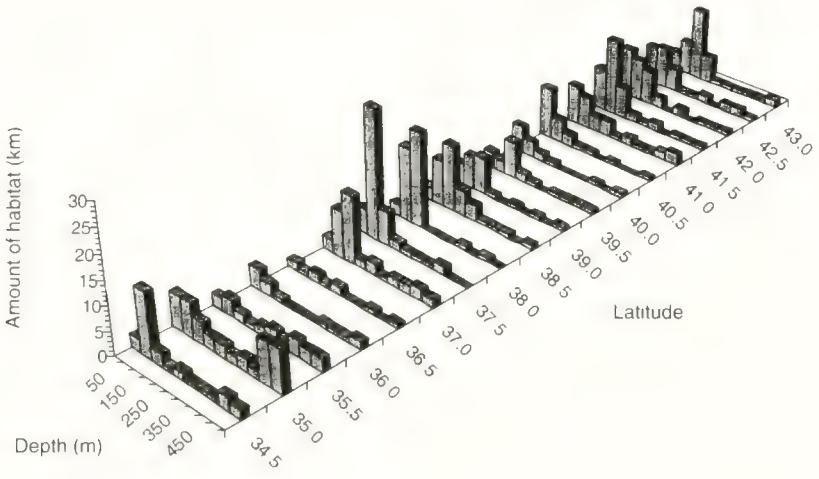

Figure 2

Estimated amount of habitat (km) at half degree latitude intervals and depths of 50–500 m.

Species groupings or assemblages were also determined by partitioning cluster analysis, rather than using other commonly employed hierarchical cluster analyses (e.g. Rogers and Pikitch, 1992; Weinberg, 1994; Mahon et al., 1998). Hierarchical cluster techniques result in dendrogram trees whose shape and structure depend largely on the division and linking methods used, frequently resulting in little similarity among the many methods (Johnson and Wichern, 1992; Ripley, 1996). Results from this type of analysis are often reported for a single method, indicating results consistent with the analyst's expectations, while neglecting to report the range of variability produced by the other alternative hierarchical methods. A more objective method of determining groupings is to use a partitioning technique such as the classical k-means algorithm (Hartigan and Wong, 1979), where the number of groups (k) is specified *a priori* and a single solution to the grouping structure is determined.

For our partitioning analysis we used a more robust variant of the k-means method, which is termed k-medians (Kaufman and Rousseeuw, 1990). The k-means and k-medians methods rely on the minimization of the (dis)similarity between cluster centers and their members. Specifically, the k-means algorithm minimizes the squared (dis)similarities, and k-medians minimizes the untransformed (dis)similarities, resulting in a measure that is less sensitive to extreme values (Kaufman and Rousseeuw, 1990; Ripley, 1996). In our study a range of k's or cluster numbers was evaluated and the best grouping structure for the data was determined according to the highest average silhouette measure (Rousseeuw, 1987). To detect misclassifications, the final rockfish assemblage structure was compared to the several dimensions obtained from the MDS ordination analysis and to our mapped CPUE distributions.

Results

There are a number of large-scale bathymetric features in the Eureka, Monterey, and Conception INPFC areas that may influence the distribution and abundance of shelf and slope rockfish species. For example, the Mendocino Escarpment is a large fracture zone that forms a huge submarine ridge near Cape Mendocino that extends nearly 2500 km westward into the Pacific Ocean and that measures 100 km across at its widest point. Well to the south of the escarpment are a number of large submarine canyons in the region of Monterey Bay and Point Sur. These submarine features, including Monterey and Sur Canyons, result in a coastal bathymetry characterized by limited shelf area and rapidly increasing depth. Farther south, in the vicinity of Point Buchon, is a large offshore area that rises to 430 m depth, i.e. the Santa Lucia Bank. Lastly, Point Conception divides zoogeographic provinces and forms the southern boundary of the area of this study.

Our restricted analysis of the bathymetry at 0.5°-latitude intervals indicates that variability in depth profiles reflects some of the important features described above. The amount of habitat in each 50-m depth interval seems to peak in the 100 to 150-m depth range for latitudes greater than 37.0°N (Fig. 2). The observed decrease in the total amount of habitat at 40.0°N, especially in waters shallower than 200 m, is due primarily to the Mendocino

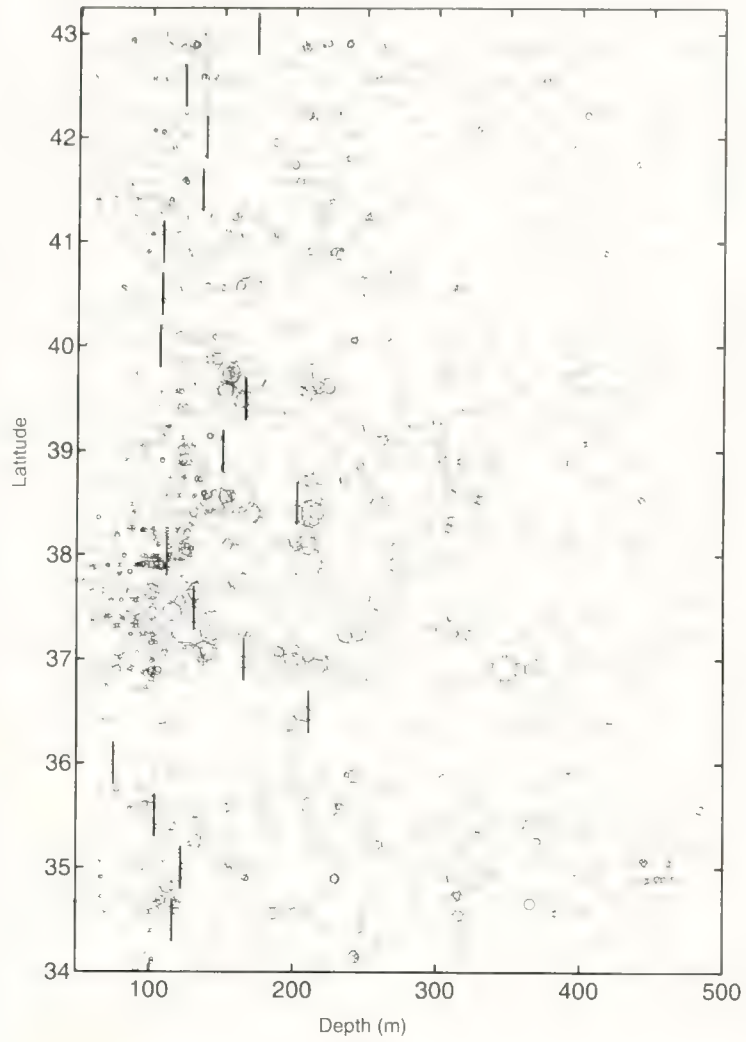

Figure 3

Plot of total rockfish CPUE estimates by depth and latitude from the AFSC triennial bottom trawl survey. Circle diameters are proportional to the square root of total rockfish CPUE. Vertical bold lines represent an estimate of the shelf break (see text).

Escarpment. Likewise, the abrupt decrease in the amount of shallow depth habitat from 35.5° to 36.5°N is directly attributable to the occurrence of submarine canyons, and the increase in habitat from 450 to 500 m at 35.0°N is due to the Santa Lucia Bank (Fig. 2). The depth at which the shelf break occurs seems to be fairly constant, generally ranging from 100 to 175 m (Fig. 3). The relatively deep (210 m) estimated shelf break at 36.5 N is due to the presence of Monterey Canyon (Fig. 3).

For the combined Eureka, Monterey, and Conception INPFC areas, the shelf trawl survey database pooled over the 1977–98 period totaled 1296 hauls that together captured 49 rockfish species, including an unidentified category (Table 1). Based on the frequency of positive trawl samples for each of the rockfish species, 26 were selected for detailed analysis (Table 1). In Table 1, the effect of changing survey sampling objectives is evident in the interannual variation in frequency of occurrence for some of the species. Perhaps most noticeable is the abrupt decline in samples of aurora (*S. aurora*) and blackgill (*S. melanostomus*) rockfish in the years 1980–92 (Table 1). Both are deep-water species and, clearly, the relatively high frequencies of occurrence in 1977, 1995, and 1998 were due to increased sampling at deeper depths that resulted from the altered objectives of the sampling design discussed earlier.

The distribution of trawl sampling locations and CPUE by depth and latitude indicated that the sampling pattern followed some of the bathymetric features mentioned above (Fig. 3). One notable feature was the paucity of samples in the 36.5°N latitude region, which was partly

Table 2

Percentage overlap of rockfish species captured in the AFSC triennial shelf bottom trawl survey by smoothed depth (50–500 m) and taken in trawls containing the species listed in the columns. POP = Pacific ocean perch.

	stripetail	chili-pepper	split-nose	short-spine	green-striped	bocaccio	short-belly	dark-blotched	aurora	widow	canary
stripetail	100	52	37	4	3	30	39	9	2	7	4
chilipepper	57	100	25	3	3	29	33	7	0	7	5
splitnose	19	12	100	7	1	8	14	12	4	1	1
shortspine	17	11	61	100	3	11	7	35	47	6	3
greenstriped	94	85	39	24	100	79	68	52	2	57	60
bocaccio	78	69	41	6	6	100	41	13	1	16	8
shortbelly	50	39	36	2	3	20	100	7	0	5	4
darkblotched	36	25	89	30	6	20	21	100	7	11	6
aurora	9	2	42	53	0	1	1	10	100	1	0
widow	84	88	36	15	23	80	49	35	1	100	36
canary	51	60	18	9	25	42	43	21	1	38	100
redbanded	52	36	99	89	14	42	32	92	30	23	15
sharpchin	88	80	52	17	18	76	57	48	1	41	25
bank	31	30	76	21	3	27	26	56	8	8	5
yellowtail	20	21	5	4	17	21	10	8	0	17	41
POP	44	11	91	64	13	28	6	98	8	17	8
blackgill	18	8	75	63	1	7	5	20	83	3	2
halfbanded	50	99	31	1	11	51	97	1	0	4	7
greenspotted	98	97	65	30	75	96	84	55	3	72	64
cowcod	100	96	97	30	20	95	93	56	7	37	21
rosethorn	81	80	95	60	40	93	61	94	12	60	36
brown	14	57	18	3	20	91	12	2	0	35	54
copper	24	19	16	5	13	33	15	2	0	15	72
vermilion	71	83	47	23	21	79	65	21	7	28	36
redstripe	21	17	18	15	21	17	21	16	1	19	24
yelloweye	97	96	80	37	52	89	72	76	2	91	57

due to the precipitous Big Sur coastline, with its marked reduction in the amount of trawlable habitat in the 50–500 m depth range. Morever, the 1980, 1983, and 1986 surveys did not sample south of Monterey Bay. Similarly, the increase in the number of samples in the 37.0–39.0°N area (Fig. 3) was attributable to an increase in the total amount of shelf habitat in that region (Fig. 2). Starting at the shallowest depths, there was a tendency for the size of the total rockfish catch to increase to a maximum in deeper waters just beyond the shelf break (~200 m), followed by a slight decrease in catch in the deepest waters (Fig. 3). Not apparent to the eye in Figure 3 is a slight, but significant trend in the distribution of sample locations towards deeper waters at more southerly sites (linear slope=–0.26, P-value=0.0041). This was probably due to the decreasing amount of shelf habitat and the increasing quantity of slope habitat as one moves south along the California coast (Fig. 2).

The amount of interspecific overlap in spatial distributions among the subset of 26 species differed, depending on whether co-occurrence was assessed from a categorization of the catches into depth-latitude intervals or by specific trawl locations (Tables 2 and 3). As expected, depth-latitude overlaps were greater than the site-specific trawl catch overlaps, due to the effect of spatial smoothing. Inspection of the depth-latitude species overlaps (Table 2) indicated that stripetail (*S. saxicola*), splitnose, chilipepper (*S. goodei*), bocaccio, and shortbelly (*S. jordani*) rockfish were most widespread with respect to co-occurrence with other rockfishes. Similarly, overlaps measured from actual trawl catches indicated that bocaccio, chilipepper, stripetail, canary, and widow rockfish have relatively high likelihoods of co-occurring with other rockfish species (Table 3).

The spatial distribution of rockfish over the continental shelf and slope generally indicated a ridge of increased diversity at approximately 250 m depth, at least for samples taken at northern latitudes (38.0–43.0°N) (Fig. 4). In contrast, for southern latitudes (34.0–38.0°N), the ridge of high diversity veered well offshore to a depth of 450

Table 2

latitude (34.0–43.0°N) locations. Individual table elements represent the percentage of occurrence of a species (reading across the row)

red-banded	sharp-chin	bank	yellow-tail	POP	black-gill	half-banded	green-spotted	cow-cod	rose-thorn	brown	copper	vermilion	red-stripe	yellow-eye
1	7	5	2	2	1	1	1	2	1	0	0	0	0	0
1	7	5	2	0	1	2	1	2	1	0	0	0	0	0
1	2	6	0	2	3	0	0	1	0	0	0	0	0	0
12	6	16	2	11	23	0	1	2	2	0	0	1	1	1
13	47	14	45	15	3	6	12	11	9	0	2	3	7	8
3	16	11	4	3	1	2	1	4	2	0	0	1	0	1
1	6	5	1	0	1	2	1	2	1	0	0	0	0	0
10	15	35	2	14	6	0	1	4	3	0	0	0	1	1
4	0	7	0	2	33	0	0	1	0	0	0	0	0	0
8	42	17	17	8	2	1	5	8	5	0	1	2	2	6
5	27	10	44	4	2	1	4	5	3	0	4	2	3	4
100	23	47	5	28	33	1	5	8	12	0	0	4	3	3
8	100	26	8	13	1	0	3	8	7	0	0	1	4	5
8	13	100	0	4	10	0	1	6	3	0	0	1	0	2
2	8	1	100	3	0	1	2	1	1	1	2	1	6	2
21	28	16	6	100	2	0	1	0	4	0	0	0	3	4
12	2	21	0	1	100	0	1	2	2	0	0	1	0	0
2	2	2	6	0	0	100	4	4	0	0	3	14	0	0
26	54	43	33	6	11	13	100	44	21	0	4	16	3	18
14	38	57	3	1	11	4	14	100	20	0	1	4	0	2
49	80	61	15	19	17	1	16	48	100	0	0	3	9	12
5	3	1	76	0	0	7	1	6	0	100	64	34	0	0
1	2	3	36	0	0	13	5	2	1	10	100	22	0	0
22	12	26	24	3	20	44	17	15	4	5	18	100	1	1
7	29	7	46	12	1	0	2	1	6	0	0	0	100	13
19	91	68	27	30	3	1	20	8	17	0	0	1	29	100

m, and there was some indication of a secondary increase in diversity at 150 m for the most southerly latitudes 34.0–36.0°N (Fig. 4). The distribution of species richness indicated that the existence of a distinct ridge at depths of 200–250 m—the highest portion of the ridge occurring between 36.0 and 39.0°N latitude (Fig. 5). In that region, in excess of eight distinct species co-occurred in individual trawl samples. A solitary peak in richness occurred at a depth of 500 m near 37.5°N latitude (Fig. 5). Inspection of the raw data revealed that this peak was heavily influenced by a single trawl sample, but there was no indication of a data recording error in this sample.

The spatial distribution of CPUE for each of the rockfish species is shown in Figures 6–10. The particular sequence of species in these figures corresponded to clustering results that are presented below. Careful examination of these 26 distributions revealed that the depth distributions of almost all species were not related to latitude. The sole exception to this generalization was the depth distribution for shortspine thornyhead, which showed a significant interaction between depth of capture and latitude, based on results from a two-way factorial ANOVA. For that species, depth distribution shifts into deep water at more southerly latitudes (Fig. 6).

Latitudinal boundaries of rockfish distributions appeared to be influenced by two of the main bathymetric features on the U.S. west coast. In particular, the Mendocino Escarpment (ME), located at approximately 40.4°N latitude, and Monterey Canyon (MC), located near 36.8°N latitude, appear to form distributional impediments for some of the species, and other species appeared to be distributed more uniformly across the entire latitudinal range of the study (Figs. 1, 6–10). Examples of species whose distributional boundaries appeared to be influenced by the ME were blackgill rockfish (*S. melanostomus*), Pacific ocean perch, chilipepper (*S. goodei*), shortbelly rockfish (*S. jordani*), bocaccio, and greenspotted rockfish. Species whose distributions appeared to border on MC were dark-blotched, greenstriped, canary, yellowtail, widow, sharpchin, and rosethorn rockfish (Figs. 6–10).

Table 3

Percentage overlap of rockfish species captured in the AFSC triennial shelf bottom trawl survey. Individual table elements represent Pacific ocean perch.

	stripetail	chili-pepper	split-nose	short-spine	green-striped	bocaccio	short-belly	dark-blotched	aurora	widow	canary
stripetail	100	35	11	1	3	9	12	5	0	3	1
chilipepper	29	100	4	1	3	10	8	2	0	6	2
splitnose	10	4	100	4	0	3	3	9	1	1	0
shortspine	12	8	50	100	3	7	3	30	27	3	2
greenstriped	48	57	7	4	100	26	27	9	0	18	15
bocaccio	23	31	8	2	4	100	8	7	0	8	6
shortbelly	9	7	3	0	1	2	100	1	0	1	1
darkblotched	27	15	57	14	3	15	6	100	1	3	2
aurora	3	0	24	38	0	0	0	4	100	0	0
widow	14	29	3	1	5	14	6	3	0	100	6
canary	9	22	2	1	7	19	7	3	0	11	100
redbanded	37	21	61	53	5	33	13	51	8	7	3
sharpchin	38	47	14	4	9	46	24	10	0	20	7
bank	11	11	48	7	1	9	3	39	1	3	1
yellowtail	4	16	0	0	6	12	1	1	0	20	18
POP	25	2	44	28	6	25	4	72	1	9	2
blackgill	3	2	41	32	1	2	2	9	45	0	0
halfbanded	2	34	0	0	3	5	18	0	0	1	3
greenspot	41	72	20	6	55	52	35	5	0	32	44
cowcod	64	39	73	8	10	93	21	10	2	10	8
rosethorn	26	41	37	32	37	56	29	36	2	32	20
brown	0	2	0	0	0	47	1	0	0	56	36
copper	1	4	0	0	3	23	2	0	0	11	73
vermilion	6	14	3	1	1	31	6	2	1	11	19
redstripe	4	8	0	0	4	8	15	0	0	8	4
yelloweye	16	72	10	2	34	63	18	12	0	63	75

A general comparison of interspecific relationships, based on depth-latitude distributions, can be gathered by inspection of a plot of CPUE-weighted depth-latitude centroids (Fig. 11). From results presented in Figure 11, some species (e.g. copper [*S. caurinus*] and brown [*S. auriculatus*] rockfish) appear to have very similar depth-latitude distributions. Aurora and blackgill rockfish are clearly deep-water southern species, whereas halfbanded (*S. semicinctus*) and vermilion (*S. miniatus*) rockfish are southern species found principally in shallow water. Although this plot is useful for identifying related species by their average distribution in space, it does not fully represent actual joint co-occurrences and assemblage relationships, as does a complete multivariate community analysis.

The results of the multidimensional scaling of the fourth-root transformed CPUE data, with the Bray-Curtis similarity measure, revealed highly significant correlations of the first three dimensions with mean depth (r=0.90, P<0.0001), total CPUE$^{0.25}$ (r=–0.82, P<0.0001), and mean latitude (r=–0.74, P<0.0001), respectively. However, these first three dimensions accounted for only 39% of the total variance in the data.

The k-medians partitioning analysis was used to examine a range of k's or cluster numbers, effectively predefining the number of distinct assemblages. The best fits were determined by the highest average silhouette measures of 0.143 and 0.140 for k = 8 and k = 4, respectively (Table 4). According to Kaufman and Rouseeuw (1990) an average silhouette measure less than 0.25 does not indicate any substantial structure in the data. Despite the low average silhouette measurements, the suggested groupings of four and eight clusters were used as an initial guideline in determining distinct species assemblages. The species groups defined in Table 4 by a division into four clusters (A, B, C, and D), and further delineated in Figure 11, show that these assemblages generally follow depth and the latitude distributions of their member species.

The first three dimensions from the multidimensional scaling analysis, along with the k = 8 cluster divisions, are shown in Figure 12. The eight clusters comprising the 26

Table 3

the percentage of occurrence of a species (reading across the row) taken in trawls containing the species listed in the columns. POP =

red-banded	sharp-chin	bank	yellow-tail	POP	black-gill	half-banded	green-spotted	cow-cod	rose-thorn	brown	copper	vermilion	red-stripe	yellow-eye
1	3	1	1	1	0	0	0	1	0	0	0	0	0	0
0	4	1	2	0	0	1	1	0	0	0	0	0	0	0
1	1	4	0	1	1	0	0	1	0	0	0	0	0	0
11	4	7	1	9	10	0	1	1	2	0	0	0	0	0
1	13	1	15	3	0	1	9	2	4	0	0	0	3	2
1	10	2	5	2	0	0	1	2	1	1	0	1	1	1
0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
5	5	19	1	11	1	0	0	1	1	0	0	0	0	0
2	0	2	0	1	21	0	0	0	0	0	0	0	0	0
1	8	1	14	1	0	0	2	0	1	2	0	1	1	1
0	5	1	21	0	0	0	4	1	1	2	4	2	1	3
100	12	15	0	17	5	0	3	2	6	0	0	1	0	0
2	100	9	1	3	0	0	2	1	3	0	0	0	9	3
3	10	100	0	2	2	0	1	2	1	0	0	0	0	0
0	0	0	100	0	0	0	2	0	0	3	1	1	0	0
10	9	8	3	100	1	0	0	0	1	0	0	0	1	0
3	0	6	0	1	100	0	0	0	1	0	0	0	0	0
0	0	0	1	0	0	100	4	1	0	0	1	3	0	0
5	21	11	29	1	1	7	100	7	4	0	1	2	2	10
3	10	22	0	0	1	1	8	100	11	0	0	1	0	2
17	47	14	9	6	3	0	8	18	100	1	1	1	23	15
0	0	0	71	0	0	0	0	0	1	100	13	12	0	0
0	0	0	24	0	0	2	1	0	1	11	100	25	0	0
1	1	2	13	0	0	6	2	1	1	8	19	100	0	0
0	20	0	0	0	0	0	1	0	3	0	0	0	100	5
0	68	0	13	2	0	0	24	5	20	0	0	1	42	100

species and listed in Table 4 closely follow the ordination plots. In particular, dimensions one and three in combination showed clear segregation of the eight distinct clusters (lower panel in Fig. 12). Clearly, the A-1 group in Table 4 stands out as a distinct assemblage in the MDS ordinations (Fig. 12). Because dimensions one and three were highly correlated with depth and latitude, respectively, we concluded that the species groups are defined by depth and latitude. However, the low amount of variance explained by the dimensions, the small sample sizes for some species, and the relatively low average silhouette measures in the partitioning analysis, would indicate that some caution should be exercised when using these results. In fact, there appeared to be some discrepancies in depth-latitude distributions and partitioning groups for the rockfish species (Table 4, Fig. 11).

Group A-1 in Table 4 represents the deep-water slope species of rockfish, and the species in groups B-2 and B-3 represent the nearshore species of rockfish. The separation of halfbanded rockfish from the nearshore group suggested by the $k = 8$ clustering was likely the result of a more southerly distribution for this species than that for the other members of the group (Fig. 7). The remaining C and D groups in Table 4 represent shelf species, group C being a southern shelf group and D representing a northern shelf group. A likely misclassification in the clustering results was the inclusion of greenspotted rockfish in the northern shelf assemblage, which was not warranted by the distribution of catches shown in Figure 9. Within the C group, the separation of cowcod as an isolate in the $k = 8$ analysis was due to this species' relatively deep distribution (Fig. 8). The separation of canary and yellowtail rockfish as a distinct cluster was the result of their relatively northern distribution and their inclusion in the southern shelf species group by the partitioning analysis was probably the result of a boundary effect (Fig. 9). Lastly, the division of the northern shelf group into D-7 and D-8 subgroups, suggested by the $k = 8$ partitioning, was likely the result of differences in the survey's total catch of rockfish (MDS dimension 2), which is not evident in distributional patterns (Table 4).

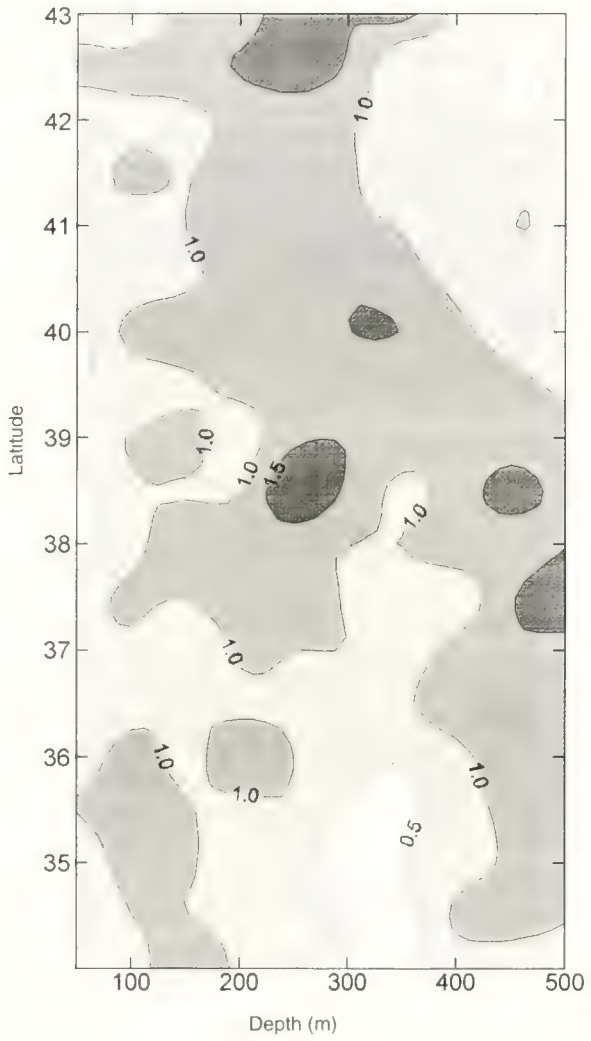

Figure 4

Contour map of Shannon-Weiner diversity indices from the AFSC triennial bottom trawl survey for all samples containing rockfish species (abundance is measured by biomass).

Table 4

Separation of rockfish species into four and eight groups, labeled by letters and numbers, respectively, based on *k*-medians analysis of AFSC triennial bottom trawl surveys from 1977 to 1998.

Group	Species	Group	Species
A-1	blackgill rockfish, aurora rockfish, shortspine thornyhead, bank rockfish, darkblotched rockfish, Pacific ocean perch, redbanded rockfish, splitnose rockfish	C-4	chilipepper, shortbelly rockfish, bocaccio, stripetail rockfish, greenstriped rockfish
		C-5	cowcod
		C-6	canary rockfish, yellowtail rockfish
B-2	copper rockfish, vermilion rockfish, brown rockfish	D-7	greenspotted rockfish, widow rockfish, sharpchin rockfish, rosethorn rockfish
B-3	halfbanded rockfish	D-8	yelloweye rockfish, redstripe rockfish

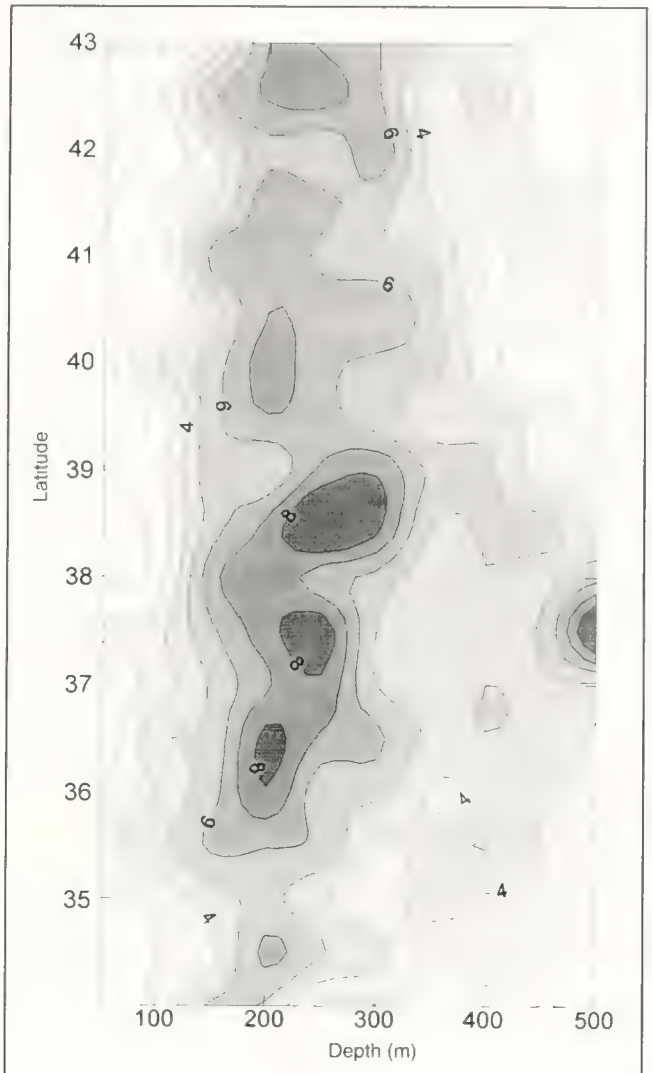

Figure 5

Contour map of species richness (number of species) from the AFSC triennial bottom trawl survey for all samples containing rockfish species.

Discussion

Our data were the result of pooling samples collected during AFSC triennial continental shelf trawl surveys conducted from 1977 to 1998. Because this interval represents a period of substantial fishery removals (Ralston, 1998), one might expect that rockfish assemblage structure changed over time as commercially important species were serially removed (e.g. bocaccio and canary rockfish). Although we did not perform year-specific analyses that would allow us to address this possibility, results from Weinberg (1994) showed that, over a comparable period of time (1977–92), the trawlable assemblages of rockfishes off Oregon and Washington were reasonably stable in composition. In particular, his year-specific recurrent group analyses revealed good agreement among surveys, from which he inferred the existence of three groups representing a deep-water assemblage (shortspine thornyhead, Pacific ocean perch, darkblotched, and redbanded (*S. babcocki*) rockfish), a mid-shelf assemblage (canary, yellowtail, and greenstriped rockfish), and a shelf-break assemblage (sharpchin, rosethorn, and redstriped rockfish). Notably, there was substantial overlap between the latter two groups, which is consistent with our findings.

It is no surprise that rockfish distributions are related to bathymetric features, particularly when viewed through bottom trawl survey samples, as we did in our study. It is noteworthy that physical barriers, particularly the Mendocino Escarpment and Monterey Canyon, seem to affect the latitudinal distribution of certain rockfishes. The former may act as a barrier to dispersal because converging currents at Cape Mendocino create conditions

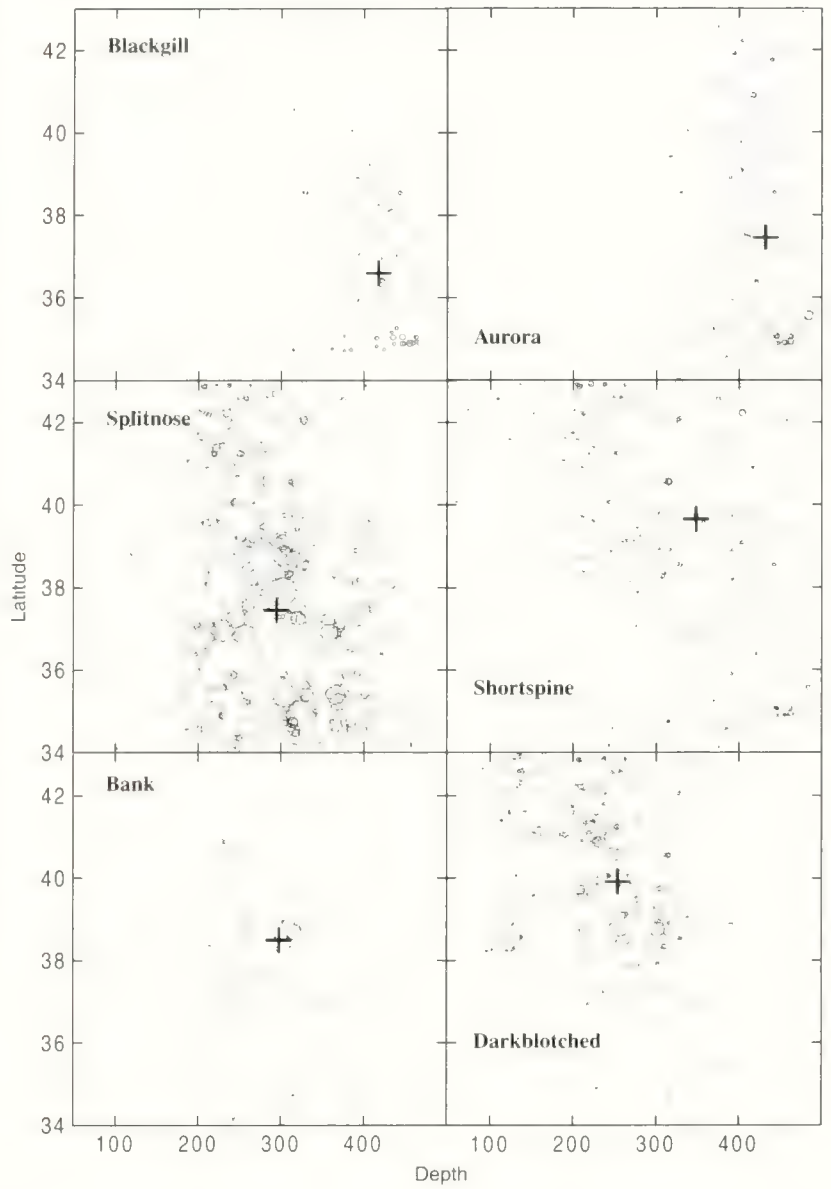

Figure 6

Plot of rockfish CPUE estimates by depth and latitude from the AFSC triennial bottom trawl survey. Circle diameters are proportional to the square root of rockfish CPUE and the bold plus symbol represents the centroid of the CPUE estimates.

that result in offshore transport (Magnell et al., 1990). Likewise, Monterey Canyon may act as a distributional barrier because continental shelf habitats constrict severely, creating a potential bottleneck to dispersion. Some support for this hypothesis is evident in the rockfish distributional maps (Figs. 6–10), which show that shallow water species are more likely to have Monterey Canyon as a distributional boundary when compared to the deeper dwelling species, for which there apparently exists ample habitat.

Overall, depth appears to be the single most important determinant of rockfish distributions. Most of the abundance patterns we observed followed the distribution of habitats by depth. Species diversity in the study area also seemed to follow the pattern of depth habitat distribution. However, species richness did not follow this pattern, but instead followed the region of overlap between shelf and slope rockfish assemblages. In fact, the contoured ridge of highest richness may be useful in spatially delineating the shelf and slope assemblages. This ridge appeared to

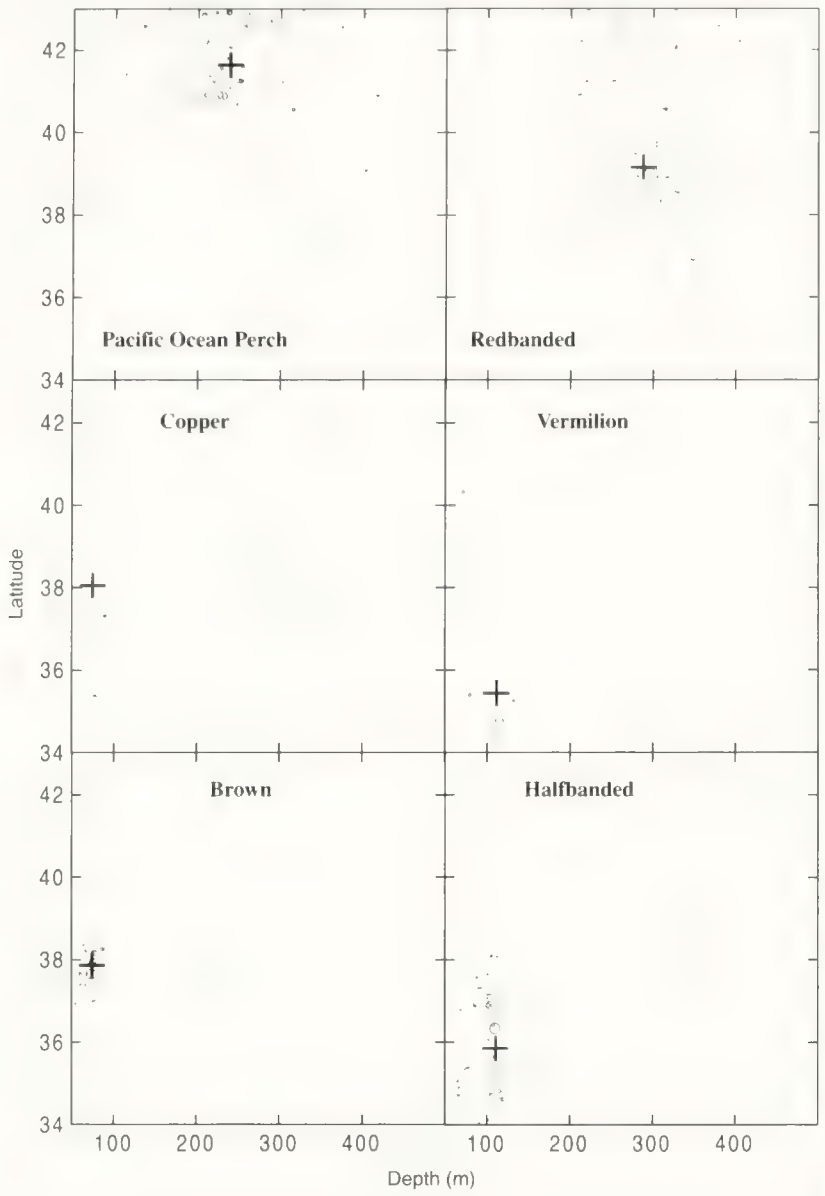

Figure 7

Plot of rockfish CPUE estimates by depth and latitude from the AFSC triennial bottom trawl survey. Circle diameters are proportional to the square root of rockfish CPUE and the bold plus symbol represents the centroid of the CPUE estimates.

be fairly constant at ~200–250 m across all latitudes included in our study.

The ridge of increased species richness indicated that there is substantial overlap in rockfish distributions. The analysis of rockfish overlap in our study was computed in two ways, i.e. by smoothed depth-latitude abundance and by raw trawl catches. The smoothed species-specific abundance estimates for all depth-latitude combinations could not be presented here because of space limitations. However, such data could be useful for detailed spatial analyses of rockfish co-occurrences in future analyses. The trawl-catch overlap data represent the best estimate of bottom trawl co-occurrence probabilities for the study area. A potential limitation of the overlap estimates presented in our study is that they came from only one survey, which employed a single sampling gear. However, the bottom trawl gear used in the AFSC triennial survey is generally similar to the fishing gear used by commercial fishermen, and previous studies have shown that catch rates from the continental shelf bottom trawl survey closely match commercial catch rates (Fox and Starr,

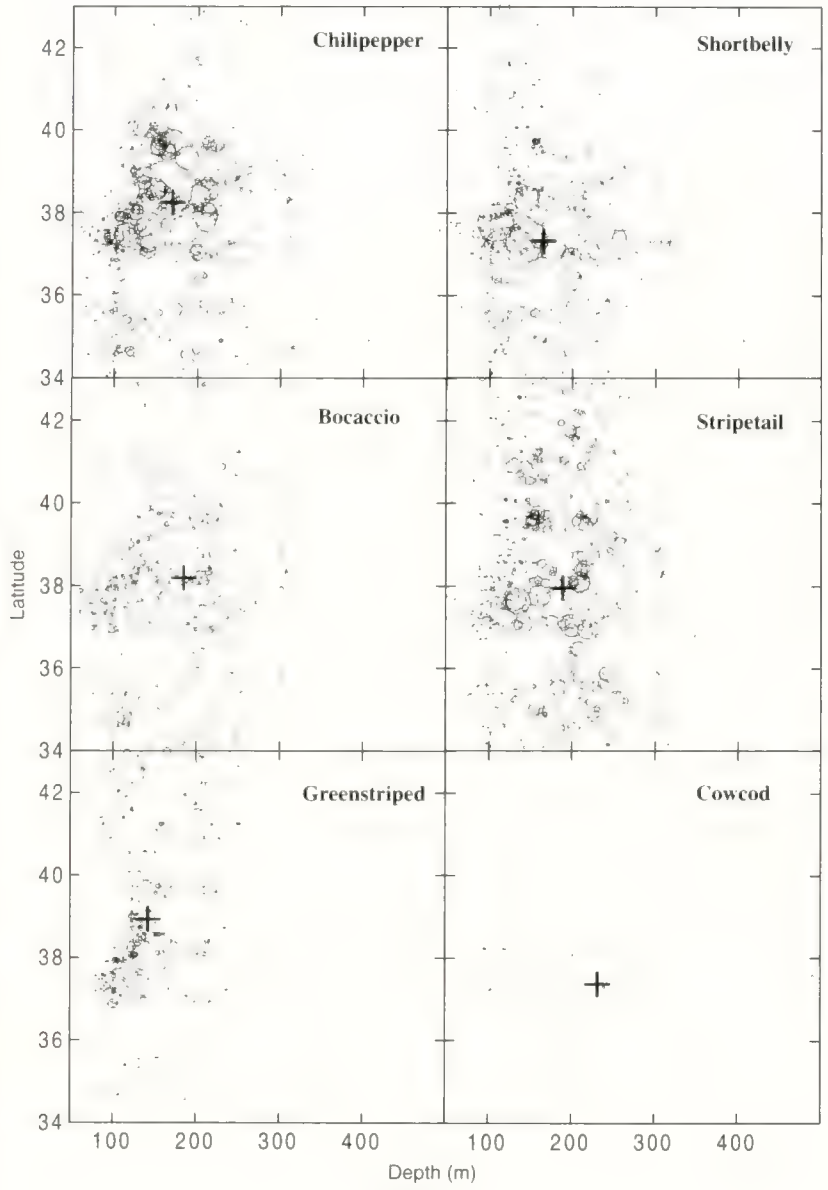

Figure 8

Plot of rockfish CPUE estimates by depth and latitude from the AFSC triennial bottom trawl survey. Circle diameters are proportional to the square root of rockfish CPUE and the bold plus symbol represents the centroid of the CPUE estimates.

1996). Another potential criticism of bottom trawl gear is its selectivity for capturing demersal fishes. Of the rockfishes included in our analysis, shortbelly and widow rockfish are two species that are known to be distributed in the water column (Lenarz, 1980; Wilkins, 1986; Chess et al., 1988). Despite their occurrence off the bottom, however, both species were captured with regularity in the bottom trawl survey (Table 1). We conclude that, at least for the trawl sector of the groundfish fishery, the results of our study should prove useful in defining assemblages for rockfish management.

As previously discussed, the assemblage descriptions given in Table 4 contain some inconsistencies with respect to the spatial distributions of the species. These apparent misclassifications may be the result of temporal variability in total rockfish abundance, as was captured by the second dimension of the MDS analysis. Because the estimated abundance of a species in our analysis was influenced by population levels of the stock at the time of each survey, which can change over time, our pooled analysis may not provide the best indication of historical assemblage asso-

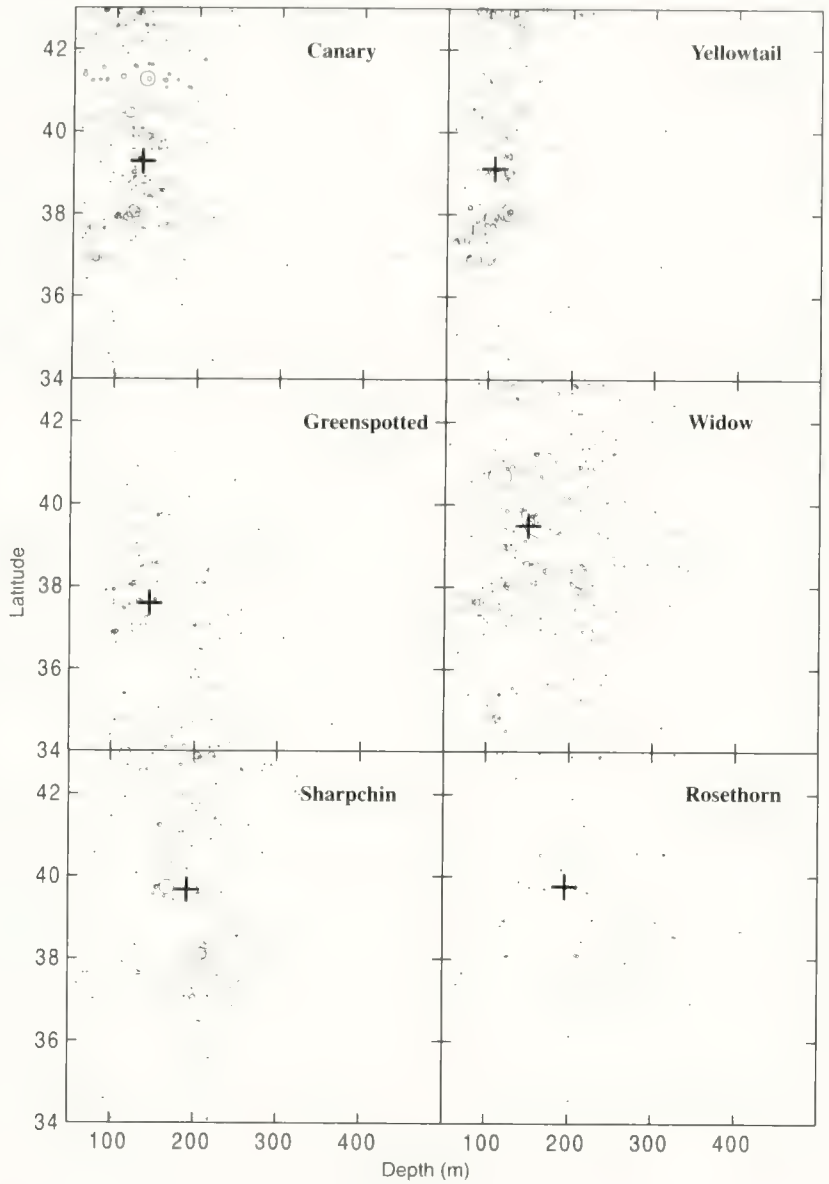

Figure 9

Plot of rockfish CPUE estimates by depth and latitude from the AFSC triennial bottom trawl survey. Circle diameters are proportional to the square root of rockfish CPUE and the bold plus symbol represents the centroid of the CPUE estimates.

ciations (see Weinberg, 1994). Furthermore, overfishing of rockfish stocks may alter spatial distributions. A good example is cowcod, which has shown a dramatic decline in abundance in recent years within the southern California Bight; most of the remaining population resides in relatively deep water (Butler et al.[3]).

Because the total abundance of each species of rockfish may have affected the results of the assemblage analysis, the species distributions were carefully re-examined and a final assemblage structure determined (Table 5). The changes from Table 4 for the k=4 groups include the placement of greenspotted rockfish into the southern shelf assemblage and canary and yellowtail rockfish into the

[3] Butler, J. L., L. D. Jacobson, J. T. Barnes, H. G. Moser, and R. Collins. 1999. Stock assessment of cowcod. *In* Pacific Fishery Management Council, Status of the Pacific Coast groundfish fishery through 1999 and recommended biological catches for 2000: stock assessment and fishery evaluation. Pacific Fishery Management Council, 2130 SW Fifth Ave., Suite 224, Portland, Oregon 97201.

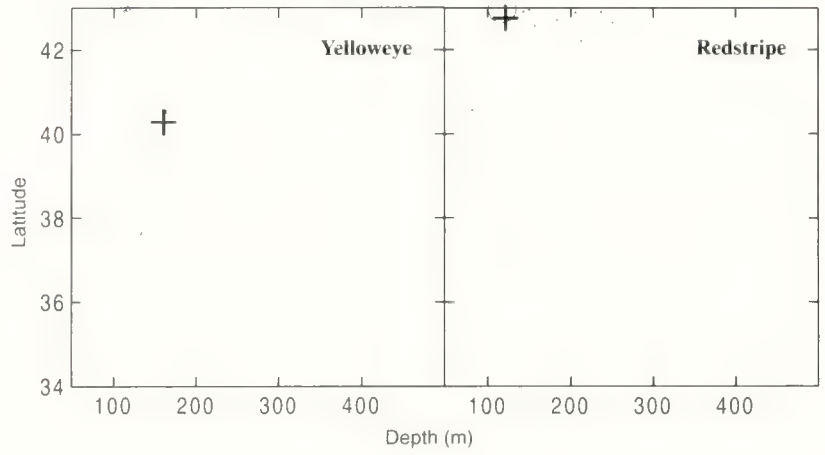

Figure 10

Plot of rockfish CPUE estimates by depth and latitude from the AFSC triennial bottom trawl survey. Circle diameters are proportional to the square root of rockfish CPUE and the bold plus symbol represents the centroid of the CPUE estimates.

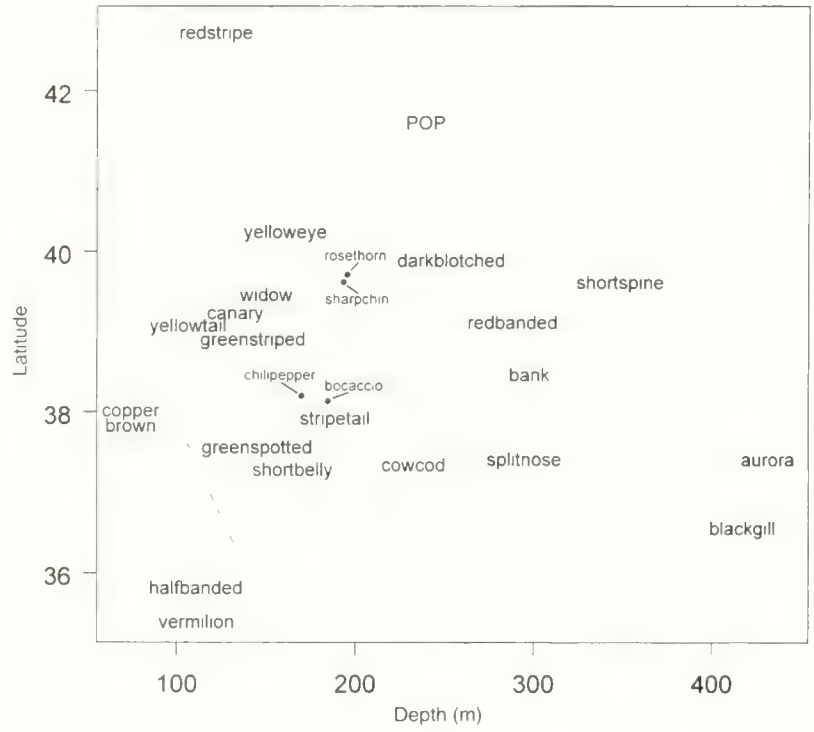

Figure 11

Plot of CPUE weighted mean depth and latitude for 26 rockfish species (center of names correspond to point estimates except for labeled points) from the AFSC triennial bottom trawl survey. Lines indicate divisions of species into clusters based on a k-medians (with k=4) partitioning analysis (see text).

northern shelf assemblage. Greenspotted rockfish has a distribution that clearly warrants its inclusion in the southern shelf assemblage. Canary and yellowtail rockfish were placed into the northern shelf assemblage because of their known abundance in northern waters outside the area of our study (see Weinberg, 1994).

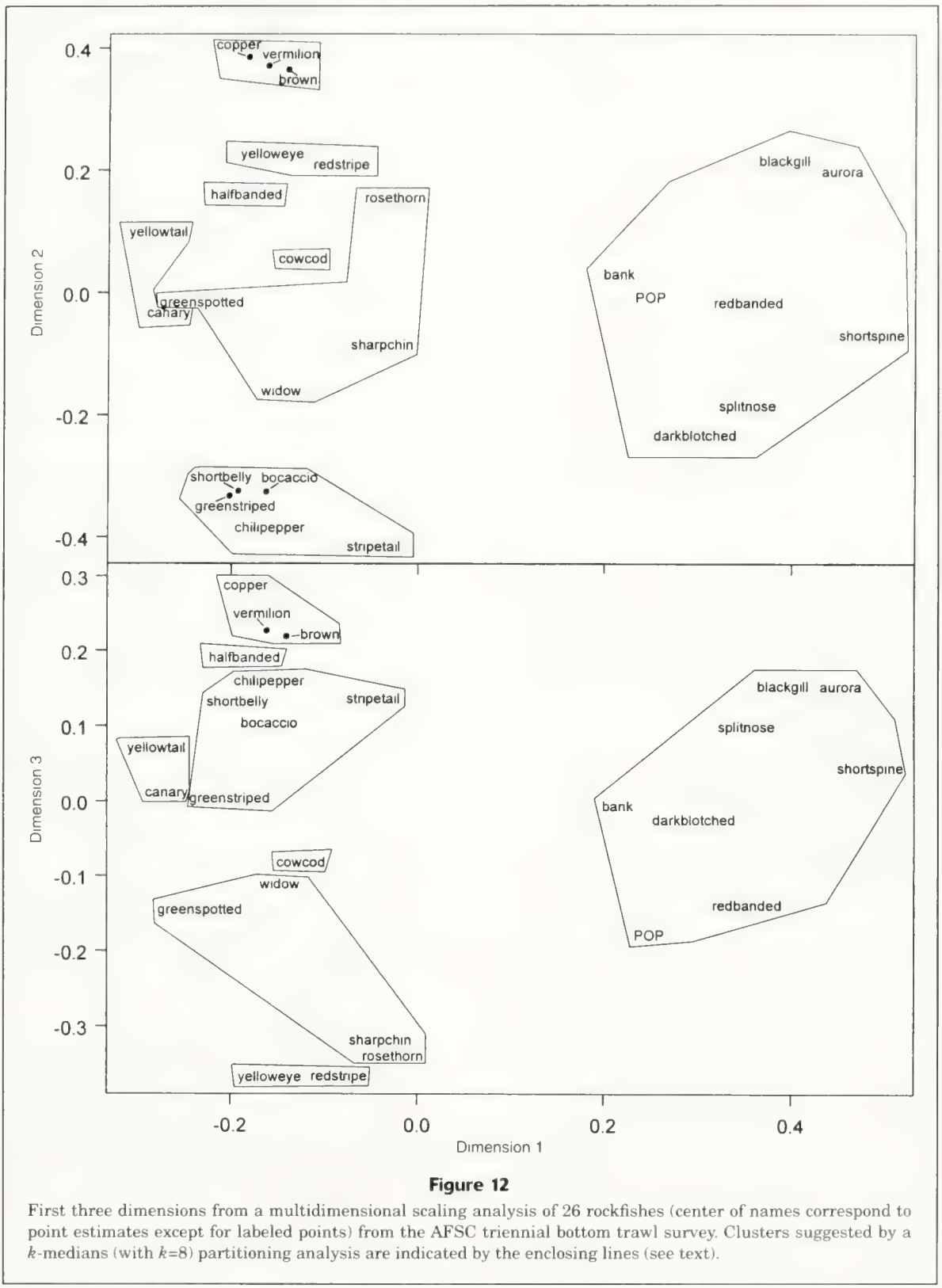

Figure 12

First three dimensions from a multidimensional scaling analysis of 26 rockfishes (center of names correspond to point estimates except for labeled points) from the AFSC triennial bottom trawl survey. Clusters suggested by a k-medians (with k=8) partitioning analysis are indicated by the enclosing lines (see text).

The dividing line between the assemblages based on depth and latitude was determined by visual examination of the distributions in Figures 6–10. The separation between shelf and slope species is roughly at 200–250 m; very few slope species were captured at depths less than 200 m. Most of the shelf species did not occur below 250 m,

Table 5

Suggested species assemblages based on distribution, ordination, and partitioning analyses completed in this study.

Habitat	Species
Deepwater slope	blackgill rockfish, aurora rockfish, shortspine thornyhead, bank rockfish, darkblotched rockfish, Pacific ocean perch, redbanded rockfish, splitnose rockfish
Nearshore	copper rockfish, vermilion rockfish, brown rockfish, halfbanded rockfish
Southern shelf	chilipepper, shortbelly rockfish, bocaccio, stripetail rockfish, greenstriped rockfish, greenspotted rockfish, cowcod
Northern shelf	canary rockfish, yellowtail rockfish, widow rockfish, sharpchin rockfish, rosethorn rockfish, yelloweye rockfish, redstripe rockfish

leaving the 200–250 m zone as an area of overlap for the two assemblages, which is exactly where the peak in richness occurred. The species in the nearshore assemblage seem to reside in waters less than 150 m depth. Perhaps the 100–150 m zone represents an area of overlap between the shelf and nearshore species.

Latitudinal divisions between species in the northern and southern shelf assemblages are not as well defined as those based on depth. It appears that most of the southern shelf group are uncommon above the Mendocino Escarpment (40.8°N latitude), with the exception of stripetail and greenspotted rockfish. The northern shelf species tend to range as far south as Monterey Canyon, leaving the area between Monterey Canyon and the Mendocino Escarpment as an area of overlap for these assemblages. This overlap is confirmed in the species richness contour plot which indicates the areas where the highest number of species were found in that latitude zone (Fig. 5). The only questionable assemblage assignment was the placement of greenstriped rockfish, which does not range south of the Monterey Canyon region but whose center of its distribution was observed in the 38.0°N latitude area.

Overall, the results of our study indicate that rockfish can be classified into fairly distinct assemblages based on their depth and latitude distributions. This study also provides estimates of the co-occurrence in the form of overlap measures for the important rockfish species off the coast of California. Both the assemblage and co-occurrence information should prove useful to fishery managers for modeling fishery dynamics, solving bycatch issues, establishing area closures, and determining effective marine reserves. Although our study highlights some uses of spatial information, the limited amount of data that is now available prevents a more thorough analysis of interannual variability in the distribution of species. We would therefore like to stress the importance of collecting more information describing the spatial distribution and co-occurrence of catches and the usefulness of those data in developing new strategies for managing west coast rockfish fisheries.

Acknowledgments

We gratefully acknowledge the assistance of Mark Wilkins, who instructed us on how to properly access and interpret RACEBASE, the Alaska Fisheries Science Center's relational data base in which the triennial continental shelf trawl survey data are stored. We also wish to thank Alec MacCall, Rick Methot, Ken Weinberg, and Mark Wilkins for their reviews of an early version of this manuscript.

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Properties of the residuals from two tag-recovery models*

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Researchers often use multiyear tag-recovery studies to assess fish populations; yet deriving useful stock assessment parameter estimates from the resulting data can be difficult. The reliability of those parameter estimates generally depends on data quality and meeting the assumptions inherent to the models used for analysis. As a result, practical application of multiyear tag-recovery models generally requires that a large portion of the data analysis involve investigation and evaluation of biases due to potential assumption violation.

Brownie et al. (1985) developed a class of models that has become widely used for the analysis of multiyear tag-recovery data. These models constitute a generalization of the class of models developed by Seber (1970), which have recently been resurrected as an important tool for the analysis of multiyear tag-recovery data by the development of the software program MARK (White and Burnham, 1999). Although these models are fairly simple and robust, in practical situations at least one of the assumptions is often not supported by the data.

Approaches that are commonly used to assess the fit of multiyear tag-recovery models include the formal goodness-of-fit test, Akaike's information criterion (AIC) (Akaike, 1973; Burnham and Anderson, 1992; Burnham et al., 1995) and other related measures such as quasilikelihood AIC (Akaike, 1985). Although these measures are informative about overall model fit, they do not provide any information about why a model fit is poor or which assumption(s) is (are) possibly in violation. To remedy this problem, Latour et al. (2001a) conducted a series of simulations and demonstrated that distinct patterns in model residuals will be evident if particular assumptions are violated. They discussed in detail the residuals associated with the time-specific parameterizations of the Seber (1970) and Brownie et al. (1985) models, as well as the time-specific instantaneous rates model developed by Hoenig et al. (1998).

The genesis of the work by Latour et al. (2001a) can be traced to two particular applications of multiyear tag-recovery models. Specifically, Latour et al. (2001b) analyzed tag-recovery data of red drum (*Sciaenops ocellatus*) in South Carolina and found systematic patterns along the diagonals in the upper right corner of the residuals matrix. Frusher and Hoenig (2001) applied a series of tag-recovery models to Australian rock lobster (*Jasus edwardsii*) data and found consistent patterns in the columns of the residuals matrix. In both instances, the researchers could only speculate as to the cause of these patterns in residuals. Although the simulations conducted by Latour et al. (2001a) have since provided reasonable explanations for the observed patterns, the development of those diagnostic procedures led to the discovery that the residuals associated with the time-specific Seber (1970) and Brownie et al. (1985) models are subject to several constraints.

This note contains a series of simple mathematical arguments that verify the assertions made by Latour et al. (2001a) about the residuals of the time-specific parameterizations of the Seber (1970) and Brownie et al. (1985) models. Unfortunately, the constraints inherent to the residuals of those models partially cloud a researcher's ability to assess the existence of a pattern. As such, knowledge of the inherent properties of the residuals of these models is of particular importance, especially because the time-specific parameterizations are commonly used for the analysis of tag-recovery data.

Materials and methods

Multiyear tag-recovery models

Multiyear tagging data are generally represented by an upper triangular matrix of tag recoveries. For example, the matrix for a study with I years of tagging and J years of tag-recovery would be, when $I = J$,

$$r = \begin{bmatrix} r_{11} & r_{12} & \cdots & r_{1J} \\ & r_{22} & \cdots & r_{2J} \\ & & \ddots & \vdots \\ & & & r_{IJ} \end{bmatrix}, \qquad (1)$$

where r_{ij} = the number of tags recovered in year j that were released in year i (note, $i = 1, \ldots, I; j = i, \ldots, J$).

Application of multiyear tag-recovery models generally involves constructing a matrix of expected values and comparing them to the observed

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data. The matrix of expected values corresponding to the time-specific parameterization of Brownie et al. (1985), which is referred to as model 1, takes the form

$$E_1 \begin{bmatrix} N_1 f_1 & N_1 S_1 f_2 & \cdots & N_1 (S_1 \cdots S_{J-1}) f_J \\ & N_2 f_2 & \cdots & N_2 (S_2 \cdots S_{J-1}) f_J \\ & & \ddots & \vdots \\ & & & N_I f_J \end{bmatrix}, \quad (2)$$

where N_i = the number tagged in year i;
f_i = the tag recovery rate in year i; and
S_i = the survival rate in year i.

As stated above, the Brownie et al. (1985) models constitute a generalization of those developed by Seber (1970). The only difference lies in the definition of the tag recovery rate. Specifically, Seber (1970) modeled the tag recovery rate in year i as $f_i = (1 - S_i) r_i$, where r_i is the rate at which tags are reported from killed fish in year i regardless of the source of mortality. The matrix of expected values associated with time-specific parameterization of the Seber (1970) models, which we will refer to as model 1*, takes the form (when $I = J$)

$$E_1 \begin{bmatrix} N_1(1 - S_1) r_1 & N_1 S_1 (1 - S_2) r_2 & \cdots & N_1 (S_1 \cdots S_{J-1})(1 - S_J) r_J \\ & N_2 (1 - S_2) r_2 & \cdots & N_2 (S_2 \cdots S_{J-1})(1 - S_J) r_J \\ & & \ddots & \vdots \\ - & - & - & N_I (1 - S_J) r_J \end{bmatrix}. \quad (3)$$

The data in each row of Equation 1 follow a multinomial distribution and maximum likelihood estimation can be used to derive parameter estimates from either model 1 or model 1*. Program MARK has emerged as the leading software package for deriving these estimates (White and Burnham, 1999).

Patterns in residuals

Latour et al. (2001a) manipulated a hypothetical perfect data set (i.e. the observed number of tag recoveries was equal to the expected number of tag recoveries) to simulate four specific forms of assumption violation for multiyear tag-recovery models. For each scenario, they analyzed the modified data with model 1, model 1*, and a time-specific parameterization of the instantaneous rates (IR) models (Hoenig et al., 1998) and noted any patterns in the residuals matrix that resulted from each particular assumption violation. Specifically, they found the following: 1) the presence of nonmixing (which violates the assumption that the tagged population is representative of the target population) leads to consistent patterns on the main and super diagonals of the residuals matrix (the main diagonal contains the (1,1),(2,2),...,(I,J) cells and the first super diagonal contains the (1,2),(2,3),...(I–1,J) cells in a square matrix); 2) permanent emigration from the study area of individuals within a tagged cohort (which violates the assumption that all tagged fish within a cohort are subject to the same annual survival and tag-recovery rates) leads to a pattern of negative residuals along the diagonals of the upper right corner of the residuals matrix; 3) tag-induced mortality or immediate loss of tags due to poor tagging (which violates the assumptions that tags are not lost and survival rates are not affected by tagging) leads to row patterns in the residuals matrix (note that these patterns are detectable only in the residuals matrix of the IR model); and 4) a change in the natural mortality rate (which violates the frequently imposed assumption that natural mortality is constant over time) leads to column patterns in the residuals matrix (again, this only applies to the IR model).

Constraints on residuals of model 1 and model 1*

Latour et al. (2001a) asserted without proof that the residuals associated with model 1 and model 1* are subject to several constraints. Specifically, they stated that the relationship $E_{II} = r_{II}$ always holds, regardless of the number of years of tagging and tag-recovery (note that E_{ij} is the expected number of tags recovered in year j that were released in year i). This implies that the observed data and the expected value associated with the (1,1) cell are always identical and that the residual for that cell is always equal to zero. They also stated that the residuals associated with the implicit "never seen again" category are also always equal to zero (recall that under a multinomial formulation, one of the possible outcomes is to never recapture a tagged fish). Collectively, these constraints imply that the residuals matrix derived from using model 1 or model 1* to analyze data from a study with I years of tagging and J years of tag-recovery takes the form

$$resid = \begin{bmatrix} 0.00 & (r_{12} - E_{12}) & \cdots & (r_{1J} - E_{1J}) & 0.00 \\ - & (r_{22} - E_{22}) & \cdots & (r_{2J} - E_{2J}) & 0.00 \\ \vdots & \vdots & \ddots & \vdots & 0.00 \\ - & - & \cdots & (r_{IJ} - E_{IJ}) & 0.00 \end{bmatrix}, \quad (4)$$

where r_{ij} and E_{ij} are as defined previously and the last column of the matrix represents the residuals associated with the "never seen again" category.

In addition to the aforementioned zero residuals, Latour et al. (2001a) stated that the sum of each row and each column of the residuals matrix must equal zero and that for the case when $I = J$ (i.e. the recovery matrix is square), the constraint that $E_{II} = r_{II}$ is also present (i.e. the residual associated with the (I, I) cell is always equal to zero).

In the context of searching for patterns in residuals, these constraints have the following implications. First, the presence of residuals that are constrained to be zero essentially reduces the total number of values that are available for inspection and ultimately forces conclusions about the existence of a pattern to be based on the signs of fewer residuals. For short-term tagging studies (e.g. 3–4 years), the loss of residuals for inspection makes it extremely difficult to evaluate model performance because each row, column, and diagonal of the residuals matrix already contains only a few values. Second, because the sum of each row of the residuals matrix must total zero, and

because the residuals corresponding to the "never seen again" cells are zero, it is not possible for a row pattern to be expressed in the residuals matrices of either model 1 or model 1*. This constraint renders it very difficult to detect assumption violations that are cohort-specific—the most common being tag-induced and handling mortality and short-term tag loss.

Results

To verify that the aforementioned constraints about the structure of the residuals matrices associated with model 1 and model 1* are true, we offer the following mathematical arguments. The proofs simply involve algebraic manipulation of equations involving the analytical formulae for the maximum likelihood parameter estimates (MLE) of model 1. The formulae for the MLEs were originally developed by Seber (1970) and can be applied to both to model 1 and model 1* (because r_i can be expressed as a function of S_i and f_i, the invariance property of MLEs implies that an MLE of r_i can be obtained by the transform). Hence, the proofs are developed for model 1, and we note that similar arguments could be constructed for the residuals of model 1*.

Recall that the analytical solutions for the maximum likelihood estimates of f_i and S_i from Seber (1970) and Brownie et al. (1985) are given by

$$\hat{f}_i = \frac{R_i C_i}{N_i T_i} \quad \text{and} \quad \hat{S}_i = \frac{R_i}{N_i}\frac{(T_i - C_i)}{T_i}\frac{N_{i+1}}{R_{i+1}},$$

where R_i and C_i are the row and column totals of the observed data in year i; and

$$\begin{aligned} T_1 &= R_1 \\ T_i &= R_i + T_{i-1} - C_{i-1} \qquad i = 2, \ldots, I \\ T_{I+j} &= T_{I+j-1} - C_{I+j-1} \qquad j = 1, \ldots, J - I \text{ if } J > I. \end{aligned}$$

The (1,1) cell

To show that the residual associated with the (1,1) cell is always zero, we must demonstrate that the difference between the observed and estimated expected value in the first cell is always zero. Hence, we have

$$\begin{aligned} r_{11} - \hat{E}_{11} &= r_{11} - N_1\hat{f}_1 \\ &= r_{11} - N_1\left(\frac{R_1 C_1}{N_1 T_1}\right) \text{(substituting for } \hat{f}_1) \\ &= r_{11} - C_1 \text{ (since } T_1 = R_1) \\ &= r_{11} - r_{11} = 0 \text{ (because the column total in the first recovery year is } r_{11}). \end{aligned}$$

The (I,I) cell when I = J

To show that the residual associated with the (I,I) cell is always zero when $I = J$, again we must demonstrate that the difference between the observed and estimated expected values in that cell is always zero. Hence, we have

$$\begin{aligned} r_{II} - \hat{E}_{II} &= r_{II} - N_I\hat{f}_I \\ &= r_{II} - N_I\left(\frac{R_I C_I}{N_I T_I}\right) \text{(substituting for } \hat{f}_I) \\ &= r_{II} - R_I \text{ (because } T_I = C_I) \\ &= r_{II} - r_{II} = 0 \text{ (because the row total in the final recovery year is } r_{II}). \end{aligned}$$

Column sums when I = J

To show that the column sums of the residuals matrix equal zero, we must demonstrate the column sum of the observed data equals that of the expected values. Consider the sum of the expected values associated with the I^{th} column of the recovery matrix, that is

$$Q = E_{1I} + E_{2I} + \cdots + E_{II} = N_1(\hat{S}_1 \cdots \hat{S}_{I-1})\hat{f}_I + N_2(\hat{S}_2 \cdots \hat{S}_{I-1})\hat{f}_I + \cdots + N_{I-1}\hat{S}_{I-1}\hat{f}_I + N_I\hat{f}_I.$$

Now substitute for $\hat{f}_i$ and $\hat{S}_i$ on the right hand side:

$$Q = N_1\left(\left(\frac{R_1}{N_1}\frac{(T_1 - C_1)}{T_1}\frac{N_2}{R_2}\right)\cdots\left(\frac{R_{I-1}}{N_{I-1}}\frac{(T_{I-1} - C_{I-1})}{T_{I-1}}\frac{N_I}{R_I}\right)\right)\left(\frac{R_I C_I}{N_I T_I}\right) + N_2\left(\left(\frac{R_2}{N_2}\frac{(T_2 - C_2)}{T_2}\frac{N_3}{R_3}\right)\cdots\left(\frac{R_{I-1}}{N_{I-1}}\frac{(T_{I-1} - C_{I-1})}{T_{I-1}}\frac{N_I}{R_I}\right)\right)\left(\frac{R_I C_I}{N_I T_I}\right) + \cdots + N_{I-1}\left(\frac{R_{I-1}}{N_{I-1}}\frac{(T_{I-1} - C_{I-1})}{T_{I-1}}\frac{R_I}{N_I}\right)\left(\frac{R_I C_I}{N_I T_I}\right) + N_I\left(\frac{R_I C_I}{N_I T_I}\right).$$

Cancel terms and factor out the term $\frac{C_I}{T_I}$:

$$Q = \left(\frac{C_I}{T_I}\right)\left[\left(\frac{R_1(T_1 - C_1)}{T_1}\right)\left(\frac{T_2 - C_2}{T_2}\right)\cdots\left(\frac{T_{I-1} - C_{I-1}}{T_{I-1}}\right) + \left(\frac{R_2(T_2 - C_2)}{T_2}\right)\left(\frac{T_3 - C_3}{T_3}\right)\cdots\left(\frac{T_{I-1} - C_{I-1}}{T_{I-1}}\right)\right] + \cdots + \left(\frac{C_I}{T_I}\right)\left[\left(\frac{R_{I-1}(T_{I-1} - C_{I-1})}{T_{I-1}}\right) + R_I\right].$$

Systematically factor out terms of the form $\frac{(T_i - C_i)}{T_i}$ (recall that $T_1 = R_1$):

$$Q = \left(\frac{C_I}{T_I}\right)\left[\left(\frac{T_{I-1} - C_{I-1}}{T_{I-1}}\right)\left[\left(\frac{T_{I-2} - C_{I-2}}{T_{I-2}}\right)\right.\right.$$

$$\left.\left.\cdots\left[\left(\frac{T_2 - C_2}{T_2}\right)(R_1 - C_1 + R_2) + R_3\right] + R_4\right] + \cdots + R_{I-1}\right] + R_I\Bigg].$$

Utilize the definition of $T_i = R_i + T_{i-1} - C_{i-1}$ to systematically simplify and cancel starting with the innermost parenthetic expression:

$$Q = \left(\frac{C_I}{T_I}\right)\left[\left(\frac{T_{I-1} - C_{I-1}}{T_{I-1}}\right)T_{I-1} + R_I\right]$$

$$-\left(\frac{C_I}{T_I}\right)\left[T_{I-1} - C_{I-1} + R_I\right]$$

$$-\left(\frac{C_I}{T_I}\right)T_I = C_I = r_{1I} + r_{2I} + \cdots + r_{II},$$

which demonstrates that the column sum of expected values equals the column sum of observed recoveries, as desired for the I^{th} column. Similar arguments hold for the other columns.

Column sums when $I > J$

The proof that the column sums of the residuals matrix equal zero when the recovery matrix is nonsquare is similar to the proof above except for making use of the definition $T_{I+j} = T_{I+j-1} - C_{I+j-1}$.

Row sums when $I = J$

To show that the row sums (excluding the "never seen again" cell) of the residuals matrix equal zero, we must demonstrate the sum of the observed data equals that of the expected values. Consider the sum of the expected values associated with the first row of the recovery matrix:

$$Q = E_{11} + E_{12} + \cdots + E_{1I} = N_1\hat{f}_1 + N_1\hat{S}_1\hat{f}_2 + \cdots + N_1(\hat{S}_1 \cdots \hat{S}_{I-1})\hat{f}_I.$$

Now substitute for $\hat{f}_i$ and $\hat{S}_i$ on the right hand side:

$$Q = N_1\left(\frac{R_1C_1}{N_1T_1}\right) + N_1\left(\frac{R_1}{N_1}\frac{(T_1 - C_1)}{T_1}\frac{N_2}{R_2}\right)\left(\frac{R_2C_2}{N_2T_2}\right) +$$

$$\cdots + N_1\left(\left(\frac{R_1}{N_1}\frac{(T_1 - C_1)}{T_1}\frac{N_2}{R_2}\right)\cdots\right.$$

$$\left.\left(\frac{R_{I-1}}{N_{I-1}}\frac{(T_{I-1} - C_{I-1})}{T_{I-1}}\frac{N_I}{R_I}\right)\right)\left(\frac{R_IC_I}{N_IT_I}\right).$$

Cancel and factor out the term $T_1 - C_1$ (recall that $T_1 = R_1$):

$$Q = \left(\frac{R_1C_1}{T_1}\right) + (T_1 - C_1)\left[\frac{C_2}{T_2} + \left(\frac{T_2 - C_2}{T_2}\right) + \right.$$

$$\left.\cdots + \left(\frac{T_2 - C_2}{T_2}\right)\left(\frac{T_3C_3}{T_3}\right)\cdots\left(\frac{T_{I-1} - C_{I-1}}{T_{I-1}}\right)\left(\frac{C_I}{T_I}\right)\right].$$

Systematically factor out terms of the form $\frac{(T_i - C_i)}{T_i}$:

$$Q = \left(\frac{R_1C_1}{T_1}\right) + (T_1 - C_1)$$

$$\left[\frac{C_2}{T_2}\left(\frac{T_2 - C_2}{T_2}\right)\left[\frac{C_3}{T_3} + \cdots + \left[\frac{C_{I-1}}{T_{I-1}} + \left(\frac{T_{I-1} - C_{I-1}}{T_{I-1}}\right)\right]\left[\frac{C_I}{T_I}\right]\cdots\right]\right].$$

The expression inside the innermost square brackets is equal to 1 (recall $T_I = C_I$). Hence, we have

$$Q = \left(\frac{R_1C_1}{T_1}\right) + (T_1 - C_1) = \frac{R_1C_1 + R_1T_1 - R_1C_1}{T_1} = R_1$$

$$= r_{11} + r_{12} + \cdots + r_{1I},$$

which shows the sum of the expected values in row 1 is equal to the sum of the observed data. Similar arguments hold for the other rows.

Row sums when $I > J$

As with the proof of the column sums when $I > J$, the defintion $T_{I+j} = T_{I+j-1} - C_{I+j-1}$ is needed to show the row sum of a nonsquare matrix (excluding the "never seen again" cells) are zero.

"Never seen again" cells

The likelihood function for the Brownie-type model is a product multinomial and the parameters for each row are constrained to sum to one. Therefore, the expected values in a row are simply an apportionment of the number tagged to the years of recovery and the "never seen again" category. Hence, the sum of the estimated expected values has to equal the row sum (including the "never seen again" cell), which implies the residuals of the "never seen again" cells are always equal to zero.

Discussion

The residuals of multiyear tag-recovery models can be very helpful for evaluating model performance. Unfortunately, examining the residuals matrix for patterns is not a commonly employed procedure for assessing model fit in practical situations. The work by Latour et al. (2001a) was intended

to demonstrate the insight a researcher can acquire by using residuals as a diagnostic probe to gauge the possibility of assumption violation. Similarly, the work presented here is intended to further guide researchers by explicitly delineating the properties of the residuals associated with two commonly applied multiyear tag-recovery models.

Model 1 and model 1* represent parameterizations of only two classes of tag-recovery models. Properties of the residuals associated with other classes of models (e.g. movement models, age-structured tag-recovery models, capture-recapture models) have not been studied. We feel strongly that similar types of insight about model performance and model fit can be acquired by examining the residuals for patterns. As such, we recommend that the residuals from other classes of models be more thoroughly investigated.

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Preliminary study on the use of neural arches in the age determination of bluntnose sixgill sharks (*Hexanchus griseus*)

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Conventional structures used for age determinations of teleost fishes (e.g. fin rays, otoliths, scales) cannot be used for elasmobranchs in which these structures are cartilaginous. However, vertebral centra with systematic deposits of calcium phosphate, have been used for age estimation in a number of elasmobranch species such as the tiger shark (*Galeocerdo cuvier*), scalloped hammerhead (*Sphyrna lewini*), and several smoothhound sharks (*Mustelus* spp.) (Cailliet, 1990). Cailliet et al. (1983) provided preparation techniques for enhancing and examining vertebral bands in these elasmobranchs. Unfortunately, the vertebral centra of a number of sharks, including bluntnose sixgill sharks (*Hexanchus griseus*), are too poorly calcified to provide age information (Cailliet, 1990). Previous attempts to age sixgill sharks by using vertebral centra have been unsuccessful (Ebert, 1986). Sharks with poorly calcified vertebral centra tend to be either deep-water species or from relatively primitive families (Cailliet, 1990). However, systematic deposits of calcium phosphate have also been found in chondrocranium, jaws, visceral arches, fin cartilage, claspers, neural and haemal arches (Clement, 1992).

Bluntnose sixgill sharks (hereafter referred to as simply "sixgill sharks") are one of the largest and most primitive species of elasmobranchs. They have a world-wide distribution and in the north-east Pacific Ocean range from the Aleutian Islands to Baja, California (Hart, 1973). Because they are deep-water inhabitants occupying depths up to 2500 m along the outer continental shelf and upper slope waters (Compagno, 1984; Ebert, 1994), little is known about their biology. Sixgill sharks are about 65–70 cm at birth and the maximum length recorded is 482 cm (Castro, 1983). They are ovoviviparous and have reported litter sizes ranging from 22 to 108 (Compagno, 1984; Ebert, 1992). The estimated size-at-maturity for females is 396 cm (Ebert, 1992), although capture of mature sixgill sharks is rare. It is likely that the young inhabit inshore waters (Compagno, 1984).

Off the west coast of Canada, an experimental fishery for sixgill sharks was initiated in the early 1990s but was terminated because of conservation concerns. Recently, there has been a renewed interest in a fishery, both commercial and sport, for the species. Incomplete knowledge regarding the biology and life history of sixgill sharks remains a concern. Given the continuing interest in a fishery (commercial and sport) and potential conservation concerns, we investigated the use of neural arches as an alternate body structure to use for the age determination of sixgill sharks. We describe the staining technique used and the bands (annuli) observed. We suggest that our technique represents a possible avenue for developing an aging technique for various elasmobranchs, particularly those with poorly calcified vertebral centra.

Methods

From May through September 1994, as part of a co-operative industry–government sixgill shark tagging program, 259 sixgill sharks were captured with hook and line gear off the west coast of Vancouver Island, British Columbia, Canada. Fishing occurred within five main areas: Kyoquot Sound (50°00′N and 127°20′W), Esperanza Inlet (49° 45′N 127°00′W), Nootka Sound (49° 25′N and 126°40′W), Tofino Inlet (49° 05′N and 125°40′W), and Barkley Sound (48°50′N and 125°20′W). A sample of ten sharks was obtained for age determination research. Total length (TL, cm) and sex were recorded for each shark.

A portion of the vertebral column containing 15–20 vertebrae, including the neural and haemal arches, was removed just posterior to the head and immediately frozen. In the laboratory the vertebral column section was thawed. The connective tissue and the outer layer of cartilage were removed from each vertebra and neural arch (Fig. 1A) by soaking them in bleach for 15 minutes and rinsing in distilled water. Some teasing away of tissue was required. For each set of vertebrae, five neural arches were separated from the vertebral centra (Fig. 1B). A single dorsoventral cut was made in each neural arch to expose the inner portions (Fig. 1B). The silver nitrate staining technique for revealing calcium deposits in vertebral centra of other shark species (Cailliet et al., 1983) was modified and applied to the neural arches. Each arch was soaked in 150 mL of 1% silver nitrate while exposed to wide spectrum light (320–400 nm). Soak times in silver nitrate varied according to the size of the arch, but all soak times lasted at least one hour. The degree of staining was assessed on an initial arch for each shark. If required, subsequent arches were restained in the silver nitrate solution and removed at 15–30 minute intervals after removal of the first arch.

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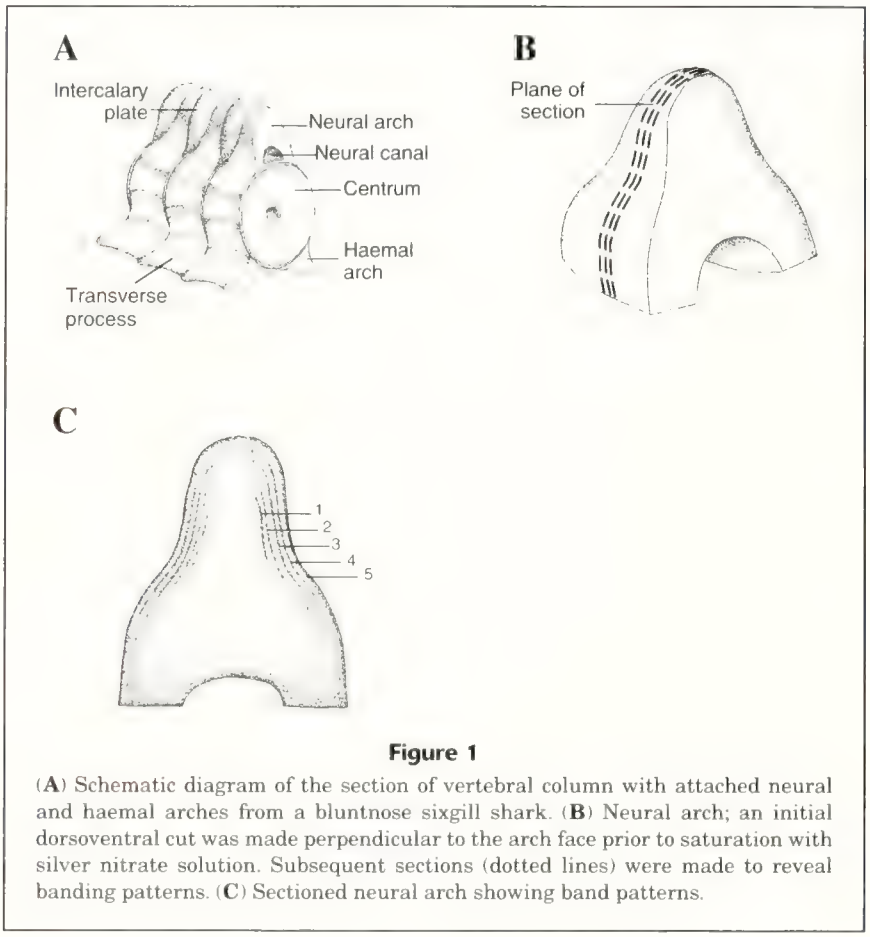

Figure 1

(**A**) Schematic diagram of the section of vertebral column with attached neural and haemal arches from a bluntnose sixgill shark. (**B**) Neural arch; an initial dorsoventral cut was made perpendicular to the arch face prior to saturation with silver nitrate solution. Subsequent sections (dotted lines) were made to reveal banding patterns. (**C**) Sectioned neural arch showing band patterns.

After soaking in silver nitrate, each neural arch was rinsed with distilled water to remove any excess solution. A scalpel was used to cut sections approximately 2–3 mm thick, parallel to the initial cut (Fig. 1B). Sections were placed under the white light (400–700 nm) of a dissecting microscope for a few minutes to allow bands to appear (Fig. 1C). A 2–3 minute soak in 5% sodium thiosulphate (Cailliet et al., 1983) was unsuccessful in halting the development process and fixing the chemical substitution of calcium salts for silver nitrate. However, a 3–5 minute soak in Kodak Stop Bath SB-1a® (1.0 L water; 125 mL 28% acetic acid) did halt the development process. The stained neural arch sections were mounted on a microscope slide with an acrylic toluene mounting medium.

Results

Of the ten sharks sampled, eight of the sharks were female (130–349 cm TL), and two were male (140 and 242 cm TL). All sharks were immature. The soak time required for the silver nitrate to penetrate the whole neural arch varied between arches of similarly sized sharks and even between arches from the same shark. Generally arches from sharks less than 200 cm TL, 200–250 cm TL, 250–300 cm TL, and greater than 300 cm TL were removed after 1, 2, 3, and 4 hours respectively. It was necessary to use several neural arches per shark in order to differentiate a clear set of bands (annuli).

The staining occurred only near the outer portion of each arch, and this left the central portion unstained (Figs. 2 and 3). Distinct, thin, dark bands were discernible in nine of the 10 sets of neural arches examined (e.g. Fig. 2). Bands in the neural arches from the 349 cm female were not all clearly defined even after soaking in the silver nitrate solution for eight hours. In general, bands appeared at regular intervals (Fig. 2). The widths between bands were asymmetrical along the whole edge of the neural arch. These widths were greater along the top edge compared to widths at the side edges (Fig. 3). In some neural arches, the bands were not continuous (Figs. 3 and 4), which made examination of different portions of the arch necessary in order to count the number of bands formed. In some arches, bands were identifiable but fainter towards the inner portions (Fig. 4). These bands appeared granular, but patterns were still detectable (Fig. 4). The number of bands increased linearly with the total length of the shark (Fig. 5). By using 67.5 cm as the median length at birth (Castro, 1983), the mean estimated growth rate was 25 cm/band (SD=4, n=9). Because all of the specimens in our study were immature, a change in the growth rate was not observed, as would be expected when size at maturity was reached.

Figure 2

A stained neural arch from a 207-cm (total length) female bluntnose sixgill shark. Note that the staining occurs along the outer third portion of the arch. Five bands are indicated by dots.

Figure 3

A stained neural arch from a 242-cm (total length) male bluntnose sixgill shark. Seven bands are indicated by dots. Note that the widths between bands are asymmetrical and the bands are discontinuous along the whole perimeter.

Discussion

The nature of the staining observed on the neural arches suggests that these structures have a potential use in the age determination of elasmobranchs. In sixgill sharks, the bands were distinct and appeared at regular intervals. The number of bands per neural arch increased with total length of the shark, suggesting their potential for age determination. The banding occurred only on the outer portions, indicating that the calcium was deposited after the proximal portion of the arches developed, probably after birth. The methodology used in our study for the staining of calcium deposits in neural arches offers some promise for age determination of sixgill sharks. Future research is required to refine the method by determining sectioning methods and thickness, optimum staining times, or perhaps alternative solution concentrations. For example, it might be more effective to cut neural arches into thin sections prior to soaking in silver nitrate rather than to soak larger portions and then section them.

Calcium deposits have been observed in the neural arches of several elasmobranchs (Cailliet, 1990). For example, Peignoux-Deville et al. (1982) provided an extensive description of these deposits for dogfish (*Scyliorhinus canicula*). However, age determination research for elasmobranchs has focused on the calcium deposits in the vertebral centra. Use of the neural arches as aging structures may provide an alternative age determination method for species in which the vertebral centra are poorly calcified

Valid age and growth information is fundamental to stock assessment and management. However, Cailliet (1990) lists only 39 species of elasmobranchs for which there are published or ongoing age verification studies. As interest and concern in commercial and recreational fishing of elasmobranchs increases, the need for age determination techniques becomes more pressing. Researchers need to investigate alternative methods for aging elasmobranchs, and we suggest that neural arches may prove to be useful. It is important to note that our observations on calcium banding in sixgill shark neural arches are preliminary and are for immature sixgill sharks only. We stress that fundamental to all aging determination studies is the validation of the method (Beamish and McFarlane, 1983), and future work is required to determine if the bands observed in our study are formed on annual, or regular, intervals.

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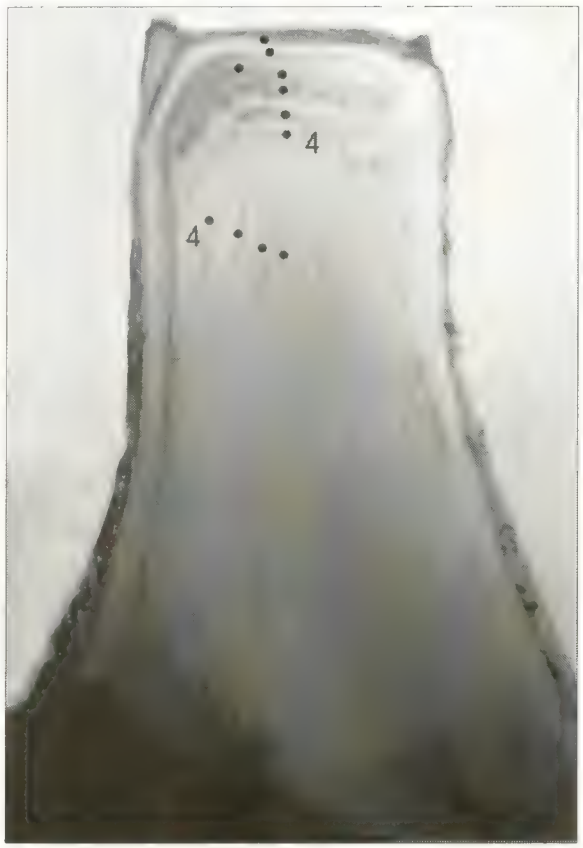

Figure 4

A stained neural arch from a 330 cm (total length) female bluntnose sixgill shark. The arch was soaked in 1% silver nitrate for 7.25 hours, but the inner portions of the arch were barely stained. Ten bands are indicated by dots, but the first four are difficult to determine. The fourth band is labelled with the number four.

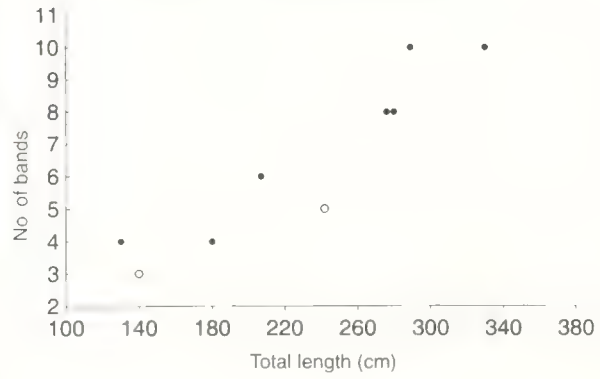

Figure 5

Number of bands observed in neural arches by total length (cm) of sixgill shark. Dots represent females; open circles represent males. As the total length of the shark increases, the number of annuli observed increases.

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Re-identification of a lamnid shark embryo

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In August 1903, a 400–500 kg pregnant female lamnid shark was caught in the Strait of Messina, Mediterranean Sea. She was reported to contain 25–30 embryos, one of which was saved and taken to the local Marine Institute, where it was subsequently examined by Sanzo (1912). The male embryo measured 36.1 cm total length (TL), weighed 800 g, and had a greatly distended abdomen, as is typical of embryos of oophagous lamnoid sharks (Gilmore, 1993). The mother and the remaining embryos were not saved. Because Sanzo was not able to examine the adult female from which the embryo was taken, the embryo was identified by a process of elimination, based mostly on morphometrics of postnatal specimens. Sanzo (1912) concluded that the embryo was a white shark, *Carcharodon carcharias* (Linnaeus, 1758). According to Sanzo (1912), the embryo was requested in 1909 by E. Giglioli and was then (in 1912) conserved at the Vertebrate Museum of the Superior Institute of Studies in Florence.

Sanzo's (1912) identification was questioned by many (Tortonese, 1950, 1956; Bass et al., 1975; Pratt[1]) but was assumed to be correct by Gilmore (1993). Tortonese (1950) suggested that the morphometric arguments used by Sanzo (1912) did not rule out the shortfin mako (*Isurus oxyrinchus* Rafinesque, 1810) but that the high fecundity of 25–30 was more consistent with *C. carcharias* than with *I. oxyrinchus* or a *Lamna species*. A lack of information on lamnid reproduction and the misidentification of a likely *Galeorhinus galeus* (Stevens[2]) with a litter of 30 as *Lamna* by Neill (1811), may have led Sanzo (1912) to consider the porbeagle *Lamna nasus* (Bonnaterre, 1788) instead of the shortfin mako as the most likely alternative to the white shark. Shann (1911) had questioned Neill's identification but this was not available to Sanzo (1912). Bass et al. (1975) incorrectly quoted Tortonese (1956) as saying that the embryo could have been a porbeagle. Tortonese (1950) pointed out that Sanzo (1912) mistook the large yolk-filled stomach (due to oophagy) for a yolk sac. Gilmore (1993) reviewed the reproductive biology of lamnoid sharks and included a redrawn sketch of the Sanzo (1912) embryo, still identified as a white shark, and also incorrectly stated that Sanzo (1912) had documented oophagy for the white shark. Francis (1996) reviewed lamnid fecundity data and showed that the shortfin mako has the highest known fecundity (18 embryos; Branstetter, 1981) in the order Lamniformes, which suggested to us that the embryo was more likely a shortfin mako.

Sanzo's (1912) embryo, well preserved in 75% ethanol, was photographed by Storai[3] in the Species Museum "La Specola" (MZUF 5911) in Florence in 1992 (Mojetta et al., 1997). The photograph—in color—suggested to us that the lost embryo had been found. This presented an opportunity for re-examining the embryo and checking Sanzo's identification.

The correct identification of the Sanzo embryo is important to our understanding of lamnid reproduction and possibly white shark conservation. Few pregnant female white sharks or embryos have been reported, and little is known about litter size, gestation period, or the timing and duration of the reproductive cycle (Uchida et al., 1987, 1996; Francis, 1996; Mollet et al., 2000). Such information is vital for understanding the population dynamics of the white shark, which is now regarded as a threatened species (Compagno et al., 1997). If the Sanzo embryo were a white shark, then it would be the smallest white shark embryo ever reported. Most have been greater than 100 cm TL (Francis, 1996; Uchida et al., 1996), although Bigelow and Schroeder (1948) reported white shark embryos in the range 20–61.6 cm TL, without giving any details. A white shark litter with embryos of 61 cm TL (5.4 kg each, Ellis and McCosker, 1991) was caught in the Mediterranean Sea (Norman and Fraser, 1938). No description of the embryos was given; however, the mass of the embryo suggested that it had a

[1] Pratt, H. L. 1996. Personal commun. Narragansett Laboratory, National Marine Fisheries Service, 28 Tarzwell Drive, Narragansett RI 02882.

[2] Stevens, J. D. 1998. Personal commun. CSIRO Marine Research, P. O. Box 1538, Hobart, Tasmania 7001, Australia.

[3] Storai, T. 1992. Personal commun. Museum of Natural Science of Valdinievole. Piazza L. da Vinci 1, Pescia PT Italy.

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Fish. Bull. 100:865–875 (2002).

substantial yolk-stomach as expected for a mid-term embryo (Mollet et al., 2000). Reports of pregnant females and small juveniles have indicated that white sharks breed in the Mediterranean (Fergusson, 1996). The reported litter size of the Sanzo shark (25–30) is the largest yet recorded for any lamnid shark. Therefore, correct identification of the embryo will also increase our knowledge of maximum fecundity in whichever species is involved. In this note, we report the results of our investigation into the identity of the Sanzo embryo. We first attempted to use morphometrics, dentition, and vertebral count and then, for unambiguous identification, we used skeletal anatomy—namely, the chondro-neurocranium, palatoquadrate, and pectoral girdle.

Materials and methods

Materials

Sanzo embryo (MZUF 5911) The preserved embryo in the "La Specola" Museum of the University of Florence, rediscovered and photographed by Storai[3] in 1992, was undoubtedly the embryo described by Sanzo (1912). Vanni,[4] curator of fishes at La Specola, provided us with the following account: "The current collection number 5911 MZUF (= Museo Zoologico Università di Firenze) corresponds to precedent n.3052 of the "Collezione Centrale dei Vertebrati Italiani" (Italian Central Vertebrate Collection), established by Giglioli in 1877 and now merged with the general collection. In the original catalogue ("libro di magazzino"), E. H. Giglioli himself wrote: "Carcharon Rondeleti ?? feto. VIII. 1903 Messina. La femmina dal quale fu tolto pesava da 400 a 500 kg e oltre a questo aveva nell'utero 25-30 altri feti nelle medesime condizioni. Avuto dal dr. Luigi Sanzo" ("Carcharadon Rondeletii ?? foetus VIII.1903 Messina.") (The female from which the embryo was taken had a weight between 400 to 500 kg and in addition to this specimen, had 25–30 other fetuses in the same condition. Presented by Luigi Sanzo" ("Carcharadon Rondeletii ?? foetus VIII.1903 Messina.")). The "Vertebrate Museum of the Superior Institute of Studies in Florence" corresponds exactly to the present "Museo Zoologico 'La Specola' dell'Università di Firenze." The "Vertebrate Museum" is actually the "Museo Zoologico 'La Specola'"; the "Superior Institute of the Studies in Florence" in 1926 became "Università degli Studi di Firenze" ("University of the Studies of Florence"). If in his paper Sanzo (1912) reported that the embryo was collected in 1903 near Messina, then undoubtedly the specimen in question is that preserved at present in the "La Specola" Museum."

Uchida embryo (SAM-35742) A 35.8-cm-TL female shortfin mako embryo was shipped to the South African Museum in Cape Town in November 2000 (SAM-35742). It came from a female (TL=3.37 m, 380 kg) that was caught near Okinawa, Japan, on 15 November 1984 (Uchida et al., 1987; Mollet et al., 2000). The litter comprised 16 embryos (11 females) with mean TL = 39.4 cm and mean mass = 1.456 kg and was preserved in formalin. A 38.4-cm-TL female embryo of this litter weighed 1.400 kg and the yolk-stomach content weighed 0.937 kg or 66.9% of the total mass (Uchida et al., 1987).

Morphometrics

Morphometric measurements of the Sanzo embryo were taken by author ADT using the methods and abbreviations of Compagno (1984). Total length (TOT) was measured with the caudal fin in the extended position. In an embryo of this size, TOT is very close to total length (TL) measured with the caudal fin in the natural position. A flexible aluminum tape was used for measurements exceeding 140 mm and rounded to the nearest millimeter. Measurements less than 140 mm were made with calipers at 0.2 mm precision. The Uchida embryo was measured six years later by authors LJVC and HFM.

We compared both our and Sanzo's (1912) measurements with the morphometrics of white sharks less than 4 m TL reported by Mollet et al. (1996) and with those of the shortfin makos summarized in Table 1. No morphometrics of white sharks of less than 1.26 m TL were available; therefore we had to use larger specimens for comparison, including two nearterm embryos reported by Francis (1996). This approach is reasonable for isometric characters, but it is inappropriate for allometric characters. The shortfin mako data included a shortfin mako litter of similar size to the Sanzo embryo (mean TL=36.2 cm, range 29.5–39.5 cm; Putz and Gilmore litter in Table 1). Morón[5] provided additional eye length data from 51 shortfin makos in Moreno and Morón (1992). We focused attention on the four morphometrics used by Sanzo (1912) to distinguish between white and shortfin mako sharks: snout shape; eye shape (EYL/EYH); ratio of mouth width to length (MOW/MOL); distance between the origins of the second dorsal and anal fins (PAL–PD2)). Our preliminary analysis indicated that eye size (EYL) and the distance between the origin of the first dorsal fin and the pectoral fin free rear tip (PD1–PRT) might be more suitable for identification and they were also included. We tested these variables graphically for their ability to distinguish between the two species (Mollet and Cailliet, 1996). The statistical program SYSTAT-SYGRAPH (Wilkinson, 1986) was used for analysis and graph production.

For specimens in which the relative positions of dorsal and anal fin origins were not measured directly, we calculated them from the difference between snout to anal fin and snout to second dorsal fin measurements (DAO=PAL–PD2). For the evaluation of the relative positions of the first dorsal and pectoral fins, we calculated the distance

[4] Vanni S. 2000. Personal commun. Sezione di Zoologia "La Specola," Museo di Storia Naturale dell'Universit, Via Romana, 17-50125 Firenze, Italy.

[5] Morón, J. 1994. Personal commun. Departamento doe Biología Animal I, Universidad Complutense de Madrid, Madrid E-28040, Spain.

Table 1

Summary of *Isurus oxyrinchus* specimens used for comparison of morphometrics with Sanzo embryo.

TL (m)	Comments	Reference
0.295	Smallest of 15 embryos [1]	Putz, Gilmore [2]
0.360	Strait of Messina, male embryo	This study [3]
0.361	Strait of Messina, male embryo	Sanzo (1912)
0.362	Mean of 15 embryos[1]	Putz, Gilmore [2]
0.395	Largest of 15 embryos [1]	Putz, Gilmore [2]
0.615	Nearterm female embryo	Stevens (1983)
0.641	Nearterm male embryo	Stevens (1983)
0.705	California, UMMZ 94726	Garrick (1967)
0.710	Smallest of 10 males and 8 females	Bass et al. (1975)
0.847	Japan, MCA 35071	Garrick (1967)
1.130	Algoa Bay, male	Smith (1953)
1.251	Smallest of 11 males and 2 females	Strasburg (1958)
1.438	New Zealand, NMNZ P.3014	Garrick (1967)
1.598	Ocean City MD, HMCZ 35899, male	Bigelow and Schroeder (1948)
1.659	Mean of 53 males and females	Moreno and Morón (1992)
1.920	South Africa, USNM 197686	Garrick (1967)
2.000	W. of Azores USNM 197706	Garrick (1967)
2.057	Mean of 11 males and 2 females	Strasburg (1958)
2.169	Mean of 13 with range 2–3 m TL	Gubanov (1974)
2.337	Bahamas, HMCZ 35367, male	Bigelow and Schroeder (1948)
2.400	Algoa Bay, male	Smith (1958)
2.579	Largest of 11 males and 2 females	Strasburg (1958)
2.692	Provincetown MA, female	Atwood (1869)
3.130	Largest of 10 males, 8 females	Bass et al. (1975)
3.210	Carmel Bay CA, female	Lea, Cailliet [4]
3.366	Santa Catalina Island Ca, female	Applegate (1966)
3.480	Redondo Beach CA, female	Seigel [5]
3.507	Anacapa Island CA, female	Applegate (1977)
3.800	Indian Ocean, female	Gubanov (1974)

[1] 15 embryos from same litter, Putz and Gilmore litter.

[2] Putz, O. 1995. Personal commun. Grolmanstrasse 48, 10634 Berlin, Germany. Gilmore, R. G. 1995. Personal commun. Dynamic Corp., Kennedy Space Center, FL 32899.

[3] Specimen identical to Sanzo (1912) embryo.

[4] Lea, R. N. 1995. Personal commun. California Fish & Game, Monterey CA 93940. Cailliet G. M. 1996. Personal commun. MLML, 8272 Moss Landing Road, Moss Landing CA 95039.

[5] Seigel, J. A. 1996. Personal commun. LACM, Los Angeles CA 90007.

between the first dorsal fin origin and the pectoral fin free rear tip (PD1–PRT = PD1 – (PP1 + P1B + P1I)). If P1B or P1I were not available for shortfin makos, we estimated (P1B + P1I) as 11% of TL (or TOT).

Tissue samples for DNA sequencing

Tissue samples were taken from the gill slits, the oral cavity, and the caudal peduncle. The samples were stored at room temperature in Wheaton polypropylene vials in 95% ethanol. DNA was extracted from the samples and polymerase chain reaction (PCR) amplification and sequencing were attempted but did not yield useful results (Bernardi[6]). This was likely due to initial fixing of the specimen in formalin (which destroys DNA) before transferal to ethanol.

X-ray analysis

For vertebral counts, we used radiographs taken initially with a Siemens Triselenix 750 (in Milan) and later with a Shimadzu R20 computerized x-ray machine for high-

[6] Bernardi, G. 1996. Personal commun. Dept. of Biology, University of California, Santa Cruz, CA 95064.

resolution radiography (in Cape Town). A pin was inserted perpendicular to the upper origin of the caudal fin to count the precaudal vertebrae. Distinct shortening of the centra was used to distinguish between monospondylic and diplospondylic vertebrae.

Dentition and mucous denticle examination

We used the term "embryonic teeth" for teeth in an embryo, which do not resemble teeth in the adult (Gilmore, 1993). We used "row" for teeth at the same developmental stage in the mesial-distal direction and "file" for teeth at different developmental stages in the labiolingual direction derived from a single locus (tooth germ) (Zangerl, 1981). We followed Applegate (1965) for the terminology anterior, intermediate, lateral, and posterior teeth and for the definition of the dental formula. This terminology and definition apply to fully formed dentition in postnatal sharks but they appeared to be applicable to the embryo under investigation. If a tooth was missing in the first row, the one behind it was counted. We used the term "mucous denticles" for dermal denticles in the oral cavity (Yano et al., 1997). We examined the mucous denticles with a Leitz DMRB microscope at 25× and 45× magnification.

The jaws could not be removed; therefore a nondestructive examination was carried out with close attention to the positions of teeth in the functional and replacement rows in the upper jaw. The functional tooth and the first replacement tooth in the fifth file (counted from the symphysis) of the upper left jaw were extracted and examined through a Leitz DMRB microscope at 25× and 45× magnification. The examination of replacement teeth required lifting the tissue that covered the developing teeth. The lower jaw was not examined as closely because only one tooth was visible to the naked eye.

We measured enameloid height (E2), if possible, for all teeth in the upper jaw (Mollet et al., 1996). We estimated the total vertical height (H) of the largest tooth, from a 25× photograph showing the outline of the root, for comparison with the likely total heights reported by Sanzo (1912). We calculated the enameloid height of each tooth in relation to the third tooth. For comparison, we estimated tooth sizes in relation to the third tooth of postnatal shortfin makos from photographs or drawings (Bigelow and Schroeder, 1948; Bass et al., 1975; Compagno, 1984).

Dissection

The Sanzo and the Uchida embryos were dissected conservatively in order to examine the internal structure of the head, jaws, and pectoral fins. The chondroneurocranium was exposed dorsally and on the left side by dissecting away flaps of skin, muscle, and connective tissue. We examined the structure of the ethmoid region, epiphysial area, orbital process, and otic capsule. Dissection of the left lateral surface of the embryo's head exposed the palatoquadrate and allowed observation of the proportions of the palatine process. Dorsal dissection of the pectoral fin allowed examination of the basal metapterygium's skeletal structure. No white shark embryo of suitable size was available for dissection and direct comparison. The white shark embryo (TL=55 cm) described by Parker (1887) was a misidentified *Carcharhinus* (Francis, 1996).

Results

General condition and morphometrics

After more than 90 years of storage in a glass container in 75% ethanol, the 36.1-cm male Sanzo embryo (MZUF 5911) was curled up, and fins and other body parts were permanently bent (Fig. 1A). The jaws appeared protruded, possibly because of the strong retraction and shrinkage of the snout. The large yolk stomach was hardened. It was 13.4 cm long, 8.6 cm wide, and 6.9 cm high and had an estimated volume of 416 cm^3. The embryo weighed 0.548 kg (condition factor, CF=11.7 kg/m^3) compared with 0.800 kg (CF=17.1 kg/m^3) reported by Sanzo (1912). The 31.5% mass loss was likely due to dehydration and dissolving and leaching of lipids from the yolk and liver into the ethanol. Despite this, the embryo did not appear to have shrunk in length because it still measured 36.0 cm TOT, 30.0 cm fork length (FOR), 27.4 cm precaudal length (PRC).

After 16 years in formalin, the female Uchida embryo (SAM-35742) looked shriveled (Fig. 1B). The embryo measured TOT = 35.8 cm, FOR = 28.8 cm, PRC = 26.6 cm, mass = 1.227 kg on 6 June 2001. The condition factor of 26.7 kg/m^3 of this embryo was similar to that calculated from the reported mean length and mass of all the embryos of the litter by Uchida et al. (1987) (CF=23.8 kg/m^3). TOT was almost the same as that of the Sanzo embryo, but this embryo weighed almost twice as much as the Sanzo embryo. Accordingly, the yolk stomach was considerably larger and was 18.5 cm long, 9.6 cm wide, and 11.5 cm high and had an estimated volume of 1069 cm^3.

Sanzo (1912) used the upturned snout, as one of four characters to distinguish his embryo from a shortfin mako, but this feature is probably an artifact of preservation (see "Skeletal anatomy" below). The three quantifiable morphometric characters used by Sanzo (1912) were also not suitable to distinguish between small white and shortfin mako sharks (Fig. 2). White sharks generally have a wider mouth, in relation to its length, than shortfin makos, but there is significant overlap (Fig. 2A). Furthermore, the ratio of mouth width to length (MOW/MOL) is allometric in small shortfin makos; mouth width becomes progressively larger than mouth length in smaller embryos. White and shortfin mako sharks both have slightly oval to round eyes and an eye length-to-height ratio between 0.9 and 1.3 (Fig. 2B). The origin of the anal fin is behind the origin of the second dorsal fin (PAL–PD2 > 0) in both white and shortfin mako sharks (Fig. 2C).

Two promising morphometrics not considered by Sanzo (1912) also proved unsuitable for identification. The first dorsal fin origin (PD1) of the Sanzo embryo was 2.3 cm (6.4% TOT) behind the pectoral fin rear tip (PRT), which suggested it might be a shortfin mako following Compagno (1984). However, the origin of the dorsal fin in both white and shortfin mako sharks varies from slightly-in-front-of

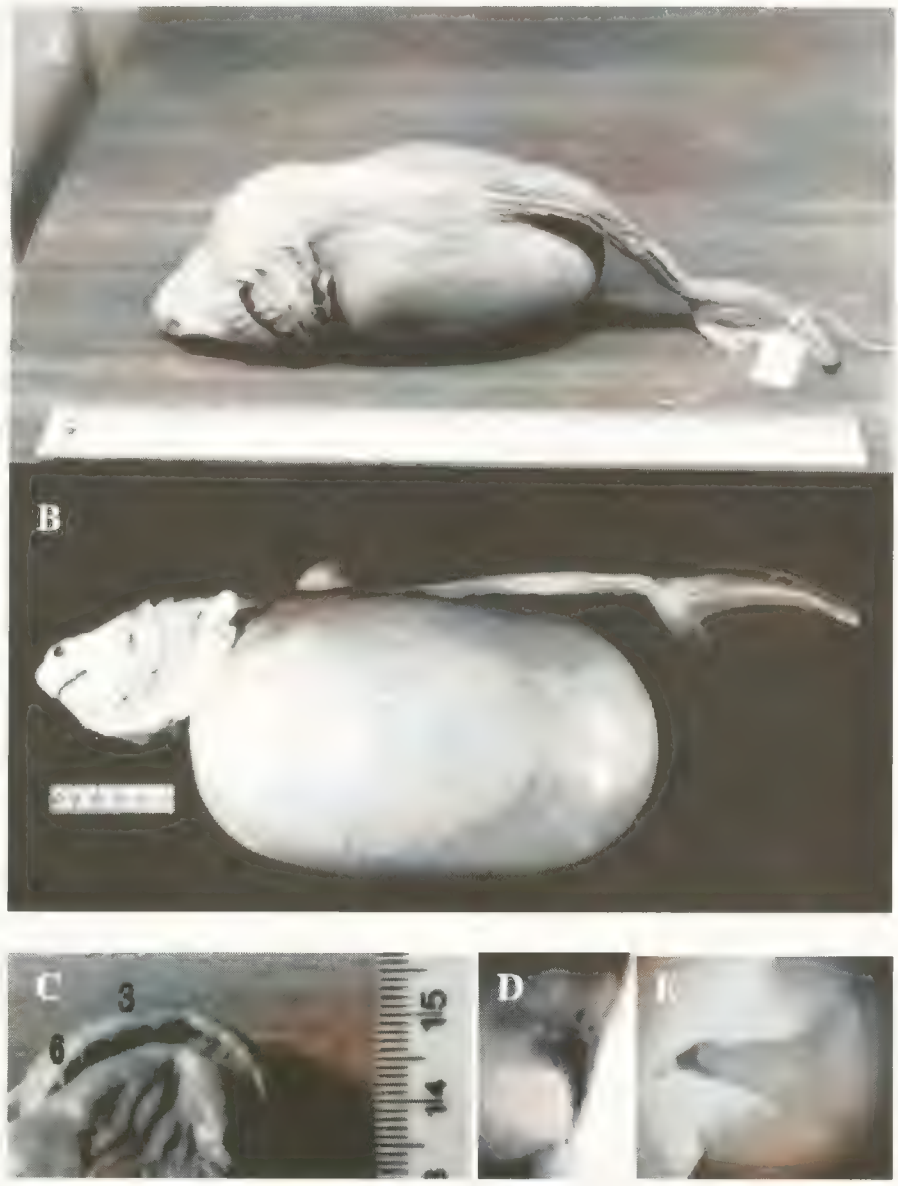

Figure 1

(**A**) Sanzo (1912) lamnid embryo (TOT 36.0 cm, MZUF 5911). Smallest scale intervals = 1/32″. (**B**) Uchida (1989) shortfin mako embryo (TOT 35.8 cm, SAM 35742). Smallest scale interval = 1 mm. (**C**) Sanzo embryo ventral view of mouth focusing on upper right teeth in first row. Smallest scale intervals = 1 mm. (**D**) Sanzo embryo functional 5th upper left tooth (enameloid height E2 ~2 mm). (**E**) Sanzo embryo replacement 5th upper left tooth (E2 ~2.3 mm, total vertical height H ~2.9 mm). Thin layer of tissue is covering apex.

to slightly-behind the pectoral fin free rear tip (Fig. 2D, PD1–PRT). The eyes of the Sanzo embryo were unexpectedly small (EYL=1.4% and 1.8%, Sanzo's (1912) and our measurement, respectively) compared with those reported for nearterm shortfin mako embryos and neonates (e.g. EYL=2.7–2.9% TL; Stevens, 1983). On the other hand, they were similar in size to those of the Uchida embryo (1.7%) and the Putz and Gilmore litter (1.4–1.8%; Fig. 2E). Small shortfin mako embryos have small eyes; but relative eye length increases rapidly and reaches a maximum of about 3% in near-term embryos of 60–64 cm TL, before declining in postnatal fish.

No secondary caudal keel was observed in the Sanzo embryo by Sanzo (1912) or by us. Nevertheless, this does not allow the elimination of the porbeagle; secondary keels may be difficult to detect in preserved porbeagle embryos

because of wrinkling of the skin (Francis, personal observ.) Lohberger (1910) did not observe a secondary keel in preserved salmon shark (*Lamna ditropis*) embryos, although this keel is present in postnatal specimens (Compagno, 1984).

Dentition

The first observations by naked eye and magnifying lens suggested a tooth formula of 8-0-7 for the upper jaw. However, the functional tooth row (i.e. the outermost row containing erect, functional teeth) of the upper right jaw was not completely filled by teeth; it comprised eight visible teeth (in file positions 2–6 and 8–10) and six gaps (in file positions 1, 7 and 11–14 (Table 2). The gaps in the functional row were indicated by the presence of teeth in the replacement rows. The gap in file 1, the broken tooth in file 2 (the 2nd tooth on the left was not erect), and the teeth in files 3–6 (labeled) are in focus in Fig. 1C. The largest functional tooth in file 6 had an enameloid height of 2.4 mm. The tooth formula for Sanzo's embryo indicated that an embryo of this size and developmental stage has the full adult complement of replacement tooth files in the upper jaw: two anteriors, one intermediate, eight laterals, and three posteriors (Table 2). The first and second replacement rows contained teeth in all file positions, indicating an eventual tooth formula of 14-0-14.

The functional tooth extracted from the 5th file in the left upper jaw (E2 ~2 mm) was fanglike and was without any lateral flattening and we considered it to be an embryonic tooth (Fig. 1D). The replacement tooth behind it was slightly curved, had little lateral flattening, and a thin layer of tissue still covered the apex (E2 ~2.3 mm and H ~2.9 mm) (Fig. 1E). We suggest that this tooth is also an embryonic tooth. The relative position of these two teeth is as shown in Figs. 1D and E.

The relative heights of the embryonic teeth in the upper jaw differed considerably from those of postnatal shortfin makos (Table 2). The first two teeth in the Sanzo embryo were much smaller than the teeth in files 3–8; the largest tooth was in file 6. In postnatal shortfin makos, the first two teeth are the largest, followed by a much smaller third tooth and smaller ones in files 4–13 (Table 2).

The tooth formula for the lower jaw was less certain. Our initial observation with magnifying lens indicated 4-0-7. Sanzo (1912) reported 4-0-4 and we agree with Sanzo that the third lower tooth was the most prominent.

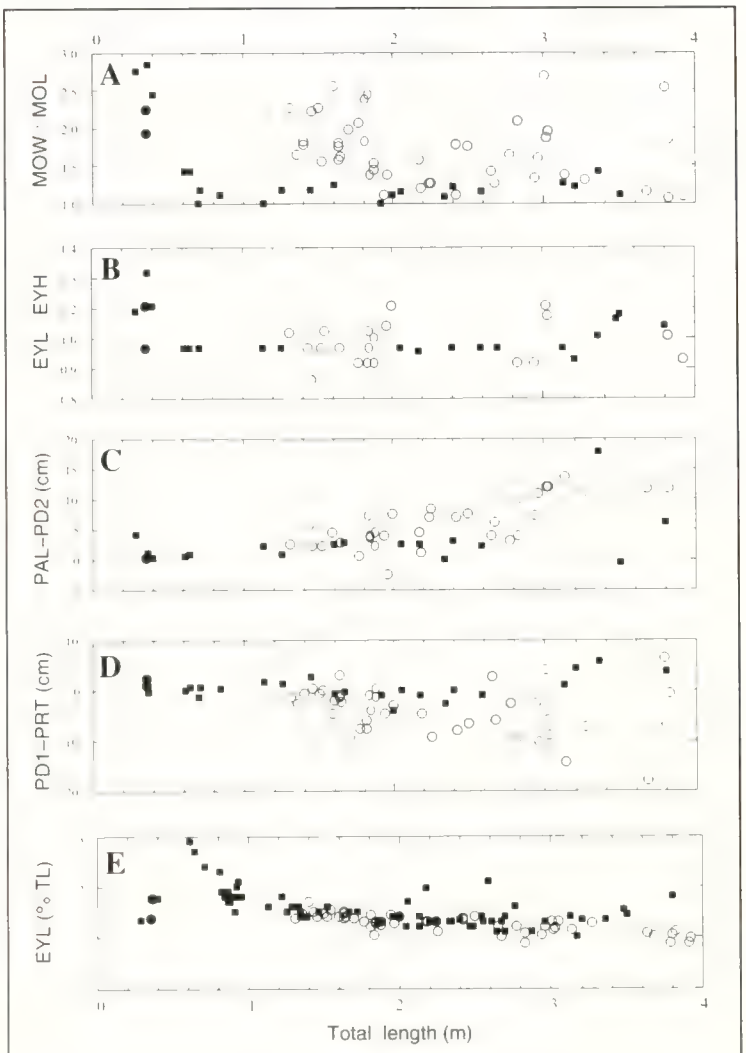

Figure 2

Relationships between selected morphometrics and total length of *Carcharodon carcharias* (open circle) and *Isurus oxyrinchus* (filled square). Sanzo embryo data (Sanzo, 1912 and our study) are indicated by dual symbols. (**A**) Ratio of mouth width to mouth length (MOW/MOL). (**B**) Ratio of eye length to eye height (EYL/EYH). (**C**) Relative position of the origins of anal and second dorsal fins (PAL–PD2). (**D**) Relative position of first dorsal fin origin and pectoral fin free rear tip (PD1–PRT). (**E**) Eye length (EYL as % TL).

Mucous denticles

Mucous denticles covered the palate and the tongue. Microscopic investigation revealed that the wartlike structures were round and had a circular, flat base and a small upward-pointing center cusp. No ridges were noted between the cusp and the base. The mucous denticles were small and far apart on the tongue, slightly larger and closer together on the palate, and largest (~0.4 mm diameter) and packed together in the region close to the cartilage of the upper jaw. There were few in the region close to the lower jaw and on the terminal part of the tongue.

Skeletal anatomy

The cranium of the Sanzo embryo differed notably from that of postnatal lamnids. The chondrocranium of the embryo was evidently damaged and foreshortened by the gen-

Table 2

Characterization of upper right dentition of Sanzo embryo (A and B) and comparison of relative tooth sizes with postnatal *Isurus oxyrinchus* (C). We report approximate enameloid height (E2) of teeth in mm. Sanzo (1912) probably reported total height. G = gap; P = present.

	File number	1	2	3	4	5	6	7	8	9	10	11	12	13	14
	Jaw position[1]	A2	A3	I	L1	L2	L3	L4	L5	L6	L7	L8	P1	P2	P3
A	Results of this study for Sanzo embryo														
	Functional row [2]	G	P[3]	1.5	1.2	2.2	2.4	G	1.4	P	P	G	G	G	G
	1st replacement row	0.7	P	P	P	2.3[4]	P	1.4	P	P	P	P	P	P	P
	2nd replacement row	P	P	P	P	P	P	P	P	P	P	P	P	P	P
B	Results of Sanzo (1912)														
	Functional row [5]	<<1	<1	<1	P	P	P	4	<1	<1	<1				
	1st replacement row								P	P					
C	Relative *Isurus oxyrinchus* teeth size in functional row														
	Sanzo (this study)	~0.4[6]	—	1.0	0.8	1.5	1.6	~0.9[6]	0.9	[7]	—	—	—	—	—
	B&S [8], 1948	2.3	1.9	1.0	1.2	1.3	1.4	1.2	1.1	0.8	0.7	0.5	0.4	0.3	
	Bass et al., 1975	2.1	1.9	1.0	1.3	1.5	1.5	1.2	0.9	0.7	0.6	0.5	0.4		
	Compagno, 1984	2.1	1.9	1.0	1.1	1.2	1.4	1.3	1.1	0.9	0.7	0.4	0.35	0.3	

[1] A1 is missing in postnatal *Isurus oxyrinchus* (Applegate and Espinosa, 1996).

[2] Eight teeth present (P) and six gaps (G).

[3] Broken tooth, 2nd tooth on left not erect.

[4] Size estimate of upper left tooth from photograph of extracted tooth (Fig. 1D). Est. total height (H) = 2.9 mm.

[5] Tooth sizes preceded with < and << signs are estimates based on qualitative descriptions by Sanzo (1912): 1st tooth almost invisible, 2nd and 3rd tooth a little more developed than the 1st one and about equal in size, 3rd tooth almost half the size of the fourth tooth, teeth 4–7 much better developed, 7th tooth 4 mm.

[6] Based on enameloid height of first replacement tooth.

[7] Relative size could not be estimated.

[8] B&S, Bigelow and Schroeder.

eral compression of its snout. This presumably was a result of being fixed and preserved in a narrow jar, and the weight of the massive yolk stomach providing sufficient force to compress the snout. The cranium had an extremely short ethmoid region compared with that of postnatal lamnids, which was exaggerated by snout foreshortening. The rostral cartilages were only basally developed and partially crushed and had no well-developed rostral node. The protruding orbits were large but short and the otic capsules were more elongated than in postnatal lamnids.

In other features, the cranium agreed with that of the Uchida embryo and postnatal shortfin makos (Table 3). The bases of the lateral rostral cartilages were positioned on the nasal capsules, as in white and mako sharks, rather than on the preorbital processes as in *Lamna* (Compagno, 1990). The ethmoid region across the nasal capsules was relatively narrow, as in shortfin makos and porbeagles; white sharks, in contrast, have notably broad nasal capsules (Haswell, 1885; Parker, 1887; Compagno, 1990). The cranial roof of white sharks has an epiphysial bar and epiphysial fenestrum just behind the anterior fontanelle, but this is absent in postnatal crania of shortfin makos, porbeagles, and Sanzo's embryo (Compagno, 1990).

The upper jaw and the pectoral girdle of the Sanzo embryo agreed with those of the Uchida embryo and postnatal makos (Table 3). The palatine processes of the palatoquadrate were low, elongated, and ventrally bent or twisted as in shortfin makos. White sharks have higher, straight, and thicker palatine processes (Compagno, 1990). Porbeagles, postnatal shortfin makos, and Sanzo's embryo all have an unsegmented metapterygium in their pectoral fin skeletons, whereas white sharks have a transversely segmented basal metapterygium (Compagno and Gottfried, unpubl. data).

The precaudal vertebral count of Sanzo's embryo (110 centra in total, including 73 monospondylous and 37 diplospondylous centra) fell close to the average for shortfin makos, whereas white sharks and porbeagles have fewer precaudal vertebrae (Table 3). The caudal vertebrae count of Sanzo's embryo (77) falls in the range of both white sharks and shortfin makos and is slightly greater than caudal counts for porbeagles. Caudal vertebral counts from radiographs are often unreliable in newborn and late fetal sharks because of poor calcification of the posterior end of the vertebral column. The caudal vertebrae of the Sanzo embryo were difficult to count without dissection because they were small and are not expected to be fully formed until late in embryonic life (Springer and Garrick, 1964). The Uchida embryo is of similar length but is considerably heavier compared to the Sanzo embryo, but its vertebral column was insufficiently calcified and we were unable to obtain a precaudal vertebral count from the x-rays taken.

Table 3

Comparison of skeletal anatomy of the Sanzo (1912) embryo with that of the Uchida et al. (1987) *Isurus oxyrinchus* embryo, and postpartum *Isurus oxyrinchus*, *Carcharodon carcharias*, and *Lamna nasus*.

Description	Sanzo	Uchida	*Isurus oxyrinchus*	*Carcharodon carcharias*	*Lamna nasus*
Chondrocranium					
Epiphysial bar and epiphysial fenestrum just behind the anterior fontanelle	No	No	No	Yes	No
Ethmoid region narrow across nasal capsule	Yes	Yes	Yes	No	Yes
Bases of the lateral rostral cartilages positioned on the nasal capsule (not preorbital processes)	Yes	Yes	Yes	Yes	No
Upper jaw					
Palatine processes low, elongated, and ventrally bent or twisted	Yes	Yes	Yes	No	No
Pectoral girdle					
Unsegmented inner basals (metapterygium)	Yes	Yes	Yes	No	Yes
Vertebral counts					
Precaudal	110	[1]	104–114[2]	99–108[2]	83–91[2]
Caudal[3]	77	[1]	79–86	68–83	68–71[2]
Total	187	[1]	183–194[2]	172–187[2]	150–162[2]

[1] Vertebral column not sufficiently calcified.

[2] Combined ranges from Springer and Garrick (1964), Bass et al. (1975), and L. J. V. Compagno (unpublished precaudal data).

[3] Caudal vertebrae may not be fully formed in early stage embryos (Springer and Garrick, 1964).

Discussion

Skeletal anatomy and morphometrics

We had to use skeletal anatomy, including the chondroneurocranium, palatoquadrate, and pectoral girdle for unambiguous identification of the Sanzo (1912) embryo after capture data and the vertebral count suggested that the embryo might be a shortfin mako rather than a white shark. Our attempts to use morphometrics, dentition, and DNA analysis were not successful.

Sanzo (1912) correctly placed the embryo in the family Lamnidae using only morphometric criteria. Only three species of the family Lamnidae normally occur in the Strait of Messina of the Mediterranean Sea: porbeagle, white, and shortfin mako sharks (Compagno, 1984; Fergusson, 1996). However, the morphometric arguments used by Sanzo (1912) for identification to species were not characteristic, leading him to incorrectly eliminate the genus *Isurus*. The upturned snout was probably caused by distortion during preservation, and we have shown that the mouth width-to-length ratio, eye shape, and relative positions of the origins of second dorsal and anal fins are not suitable criteria for distinguishing between white and shortfin mako sharks. Other promising morphometrics also failed to distinguish between the two species. These conclusions are tentative—confirmation will depend on obtaining measurements of these characters from small embryonic white sharks, which were missing from our database.

Dentition

Tooth shape is species-specific in postnatal *Lamna*, *Isurus*, and *Carcharodon* (Compagno, 1984) but not in embryos. Lamnid embryos have specialized "embryonic" teeth that are adapted for grasping and tearing the membrane of the eggcases on which they feed (Gilmore, 1993; Francis and Stevens, 2000). We observed fanglike embryonic teeth in porbeagle embryos, which lacked the characteristic cusplets of adult specimens. We observed fanglike embryonic white shark teeth lacking serration in the intestine of a nearterm embryo similar to the embryonic teeth of the Sanzo embryo (Francis, 1996; Francis and Stevens, 2000). Embryonic teeth are similar in all lamnid embryos and do not appear to be suitable for identification. Shortfin mako embryos shed their embryonic dentition at about 45–50 cm TL and nearterm embryos have emerging adultlike teeth (Gilmore, 1993; Mollet et al., 2000).

It is difficult to describe a dentition completely without the benefit of prepared jaws, particularly in a relatively small embryo. In addition, the tooth formula of a small embryo may be different from that of a postnatal specimen. Sanzo (1912) reported an upper jaw tooth formula of 10-0-10; we observed 14-0-14, the full adult complement of replacement tooth files. That suggests that Sanzo (1912) had not observed the four replacement teeth in files 11–14. He reported two replacement teeth behind the functional teeth in files 7–8 and 8–9, whereas we observed replacement teeth in all position of two rows by pulling back the dental lamina (Table 2).

We could not resolve other discrepancies. Sanzo (1912) reported four relatively large teeth in files 4–7, the 4th one was more than twice the size of the 3rd one, and the 7th tooth was 4 mm (probably including the root). We concluded that the four largest teeth were in files 3–6 and we estimated the total height of the largest tooth in file 6 to be about 3 mm (based on E2=2.4 mm). It is possible that Sanzo's (1912) minute first tooth was a recessive parasymphysial tooth, which we overlooked or which had disappeared before we examined the embryo. Our description of the dentition of the Sanzo embryo agrees in general with that in similar-size salmon shark and porbeagle embryos (Lohberger, 1910; Mollet, personal observ.).

DNA sequencing and mucous denticles

DNA sequencing should have allowed identification of the Sanzo embryo but provided no useful results. This was likely due to initial fixing of the Sanzo embryo in formalin (which destroys DNA) before transferal to ethanol.

We did not have SEM at our disposal during the initial stage of the investigation but suggest that the mucous denticles might be suitable to identify lamnid embryos. Early development of mucous denticles is expected to occur in the oophagous lamnids (Reif, 1985; Raschi and Tabit, 1992). Reif (1985) suggested that dermal denticles are family, genus, and in some cases even species specific. Postnatal shortfin makos and white sharks have different mucous denticles (Reif, 1985; Peyer, 1968).

Capture information

The capture information provided by the fisherman who caught the Sanzo shark was more consistent with shortfin mako than with other lamnids, based on presently known lamnid reproductive biology (Francis and Stevens, 2000; Mollet et al., 2000). The litter size of 25–30 was estimated and may have been inaccurate, but it does indicate a large litter. The large litter size could be the reason that the Sanzo embryo weighed considerably less than the Uchida embryo although they had similar length. Litter size in porbeagles is nearly always four (maximum of five, Francis. 1996; Francis and Stevens, 2000). Maximum litter size in white sharks is at least ten; unconfirmed reports are as high as 14 (Francis, 1996). Shortfin makos have the largest litters yet reported in the Lamnidae, reaching at least 18 (Branstetter, 1981; Mollet et al., 2000).

The shark was estimated to weigh 400–500 kg, although this must be considered approximate. The TL of a female of this mass would be 3.58–3.85 m (Stevens, 1983; Mollet et al., 2000). A shortfin mako of this length would undoubtedly be mature (Mollet et al., 2000) and the maximum reported length is 4 m (Bigelow and Schroeder, 1948; Mollet[7]). Female white sharks do not mature until about 5.0 m (Mollet et al., 2000) with a corresponding mass of ~1200 kg (Mollet and Cailliet, 1996). A full-term litter of 25–30 shortfin makos would weigh ca. 75 kg, which would be reasonable for a female shortfin mako weighing around 500 kg (Mollet et al., 2000). A white shark litter of 25–30 would weigh about 500 kg at birth, i.e. the total mass of the female shark caught, which is not possible.

We conclude that the Sanzo embryo is *Isurus oxyrinchus*. This analysis corrects a long-standing error in the literature and should provide the incentive to procure and describe a white shark embryo of similar developmental stage to that of Sanzo's embryo. The smallest photo-documented white shark embryos were ca. 1.0–1.1 m TL (Uchida et al., 1996) and fully documented white shark embryos were all nearterm and had a TL between 1.35–1.51 m (Uchida et al., 1987, 1996; Francis, 1996). The definite identification of the Sanzo embryo suggests that the maximum litter size of the shortfin mako is likely larger than 18 (Branstetter, 1981; Mollet et al., 2000) and possibly as large as 25–30.

[7] Mollet, H. F. 1999. http://homepage.mac.com/mollet/Io/Io_large.html. [Access date: 9 August 2002.]

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Necropsy findings in sea turtles taken as bycatch in the North Pacific longline fishery

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Concern about interactions between fisheries and marine turtles has increased in recent years, particularly since East Pacific leatherback turtles (*Dermochelys coriacea*) may become extinct (Spotila et al., 2000). However, relatively little published information exists on interactions between sea turtles and North Pacific longline fisheries. The most available literature on the topic focuses on modeling data from fisheries observers for estimating the probability of animals dying and fishery-induced mortality (McCracken[1]; Kleiber[2]). A more recent study was undertaken with satellite telemetry and remote sensing to evaluate the probability of interaction between longline fisheries and loggerhead sea turtles (*Caretta caretta*) and the effects of hooking (Polovina et al., 2000; Parker, in press).

Necropsies on turtles caught by longline fisheries may provide additional objective data on the causes of mortality and the health of pelagic turtles. Although ample literature exists on evaluating the health of benthic coastal-residing immature sea turtles in Hawaiian waters (Aguirre et al., 1994; Work and Balazs, 1999), nothing is known about the health status of pelagic sea turtles because of the difficulty in locating animals (Bolten and Balazs, 1983) and the unavailability of specimens for diagnosis. Most turtles caught in longline fisheries are released alive (McCracken[1]; Kleiber[2]). The few dead turtles that area recovered can be returned to shore legally only by observers (who are present in only ~5% of the Hawaii-based North Pacific fishing fleet) (Balazs et al., 1995). Nevertheless, examining freshly dead turtles caught in longline fisheries provides a unique opportunity to gain insight into the health status and diet of pelagic sea turtles. Our objective was to systematically evaluate all available carcasses of fresh-frozen sea turtles that had been caught in the Hawaii-based longline fishery for an evaluation of their health and to document their diet.

Methods

Free-ranging marine turtles accidentally taken as bycatch by the North Pacific longline fishery were landed on the fishing vessel and evaluated for signs of life by fishery observers employed by the National Marine Fisheries Service. Sea turtles that were judged to be dead by specific criteria (Balazs et al., 1995) were stored frozen and returned to Honolulu, Hawaii, where we recorded weight (kg) and body morphometrics (cm).

Gross necropsies entailed a complete external and internal exam of all organ systems. We also recorded any identifiable stomach contents. Body condition of turtles was subjectively classified as good, fair or poor if coelomic and mesenteric fat reserves appeared ample, moderate, or sparse, respectively. Postmortem condition was classified as good, fair, or poor depending on the gross appearance of organs during the necropsy. We classified turtles as lightly hooked if the longline fish hook was lodged in the mouth or externally, or as deeply hooked if the hook was present in the gastrointestinal tract caudal to the glottis. Hooks were classified as tuna (3.6 or 3.8 mm) or swordfish and mustad (offset 8/0 or 9/0).

Tissue samples (heart, lung, kidney, liver, spleen, brain, stomach, small intestines, skin, trachea, salt gland, gonad, thyroid, pancreas, and brain) were fixed in 10% buffered formalin, sectioned at 5 µm and stained with hematoxylin and eosin for microscopic examination. Representative tissues were stored frozen (–70°C) in sterile plastic bags. Where gross necropsy findings suggested infectious or inflammatory disease, swabs or tissues were processed for microbiology. For bacteriology, swabs were plated on McConkey and blood agar and incubated at 27°C and 37°C for 48 h. For virus isolation, frozen tissues were homogenized, the supernate filtered through a 0.22-µm filter, and plated on green sea turtle embryo fibroblasts (Moore et al., 1997).

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[2] Kleiber, P. 1998. Estimating annual takes and kills of sea turtles by the Hawaiian longline fishery, 1991–97, from observer program and logbook data. Administrative Report H-98-08, 21 p. Southwest Fisheries Science Center, Nat. Mar. Fish. Serv., NOAA, 2570 Dole St., Honolulu, HI 96822.

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Table 1

Vital necropsy statistics for turtles caught by the Hawaii-based pelagic longline fishery in the North Pacific. Age are immature (I), subadult (S), and adult (A). Body and post-mortem condition were classified as good (G) or fair (F). SCL, BC, PMC, and Set stand for smallest carapace length, body condition, postmortem condition, and hook set, respectively.

ID	Species	Wt (kg)	SCL	Age	Sex	BC	PMC	Hook	Set
1	*C. mydas*	25.4	55.6	I	M	G	F	tuna 3.6-mm	light
2	*C. mydas*	50	67.9	S	F	G	G	tuna 3.6-mm	light
3	*D. coriacea*	44.5	70.4	I	F	G	G	tuna 3.6mm	light
4	*D. coriacea*	74.1	85.3	I	F	G	G	tuna 3.6-mm	light
5	*L. olivacea*	13.2	43.7	I	F	G	F	tuna 3.6-mm	light
6	*L. olivacea*	15.3	46.6	I	F	F	G	offset 8/0	deep
7	*L. olivacea*	21	54	I	F	G	G	tuna 3.6-mm	light
8	*L. olivacea*	24.5	57.5	S	F	G	G	tuna 3.6-mm	light
9	*L. olivacea*	33.4	62.1	A	F	G	G	tuna 3.6-mm	light
10	*L. olivacea*	34.1	60.4	A	F	G	G	tuna 3.6-mm	deep
11	*L. olivacea*	37.7	62.9	A	F	G	G	tuna 3.6-mm	light

Results

We performed necropsies on seven olive ridley (*Lepidochelys olivacea*), two green (*Chelonia mydas*), and two leatherback sea turtles (Table 1). Turtles were caught between 5.4–18.0°N and 148.5–161.3°W in the North Pacific from February 1996 through June 2000.

One leatherback sea turtle (identification [ID] 3) had severe acute inflammation of the liver associated with clumps of fibrin (Fig. 1, A and B), mild acute inflammation of heart muscle, and mild diffuse pulmonary edema. No bacteria or viruses were isolated from the liver. The other leatherback sea turtle (ID 4) had severe diffuse fibrosis of the pancreas (Fig. 1C) and a large subcapsular hematoma of the liver. The lesions in both turtles were severe enough to cause significant impairment of organ function and probable morbidity. Incidental microscopic lesions in four of the seven olive ridley sea turtles included mild acute heart muscle inflammation (ID 6), mild focal necrosis in one lung (ID 7), parasite-induced necrosis in the stomach wall (ID 8), and foreign material (probable ingesta) in the bronchioles (ID 10). Microscopic lesions in the olive ridley sea turtles were not severe enough to cause morbidity, and no microscopic lesions were seen in the remaining turtles including the green sea turtles.

Cause of mortality for all sea turtles was drowning after hooking; however, in only one case (olive ridley ID 11) was there gross evidence of water in the lungs. Female (10/11) and lightly hooked (9/11) animals predominated. Most hooks were tuna 3.6-mm hooks (Table 1). In one deeply hooked olive ridley turtle (ID 10), the hook perforated the esophageal wall in two places at approximately half of the length of the wall. In the other olive ridley sea turtle, ID 6 (classified as deeply hooked by the observer), the hook perforated just caudal to the tongue. Both leatherback sea turtles had been entangled by the leader; one had the leader tightly wound around the right front flipper, the other had the leader around the neck, where it had caused lacerations .

Bait (sama; *Cololabias saira*) was seen in the esophagus of four olive ridley sea turtles; one turtle contained three fish, indicating ingestion from more than one hook. Other items in olive ridley stomachs included cowfish, pyrosomas, pelagic snails, bird feathers, and small fragments of plastic. Stomachs from both leatherback turtles and from one green turtle contained pyrosomas exclusively.

Discussion

Only two sea turtles were classified as deeply hooked; most turtles had no visible lesion indicative of hooking either to the observer present on board when the turtles were hauled into the boat, or to the observer and us at the time of necropsy. Turtles that scored as lightly hooked but that died later would suggest that deep or light hooking may not be satisfactory criteria for the probability of short-term survival in the species we studied. Similarly, Polovina et al. (2000) and Parker et al. (in press) observed that there was no significant difference in distance or speed of travel between deeply and lightly hooked loggerhead turtles that were caught by the North Pacific longline fishery and then marked with satellite tags, and followed for several months. Hence, deep versus light hooking may not be a useful indicator of long-term survival for these species.

The preponderance of females in our study was noticeable. Markedly skewed sex ratios in wild sea turtles are more commonly encountered among hatchlings (Gonzales et al., 2000), presumably due to incubation well below or above the pivotal temperature (Mrosovsky and Yntema, 1980). Studies of immature green sea turtles stranded with fibropapillomatosis in Hawaii revealed a sex ratio of close to 1:1 (Koga and Balazs, 1996). Ross (1984) in Oman reported sex ratios of adult green sea turtles to be closer to

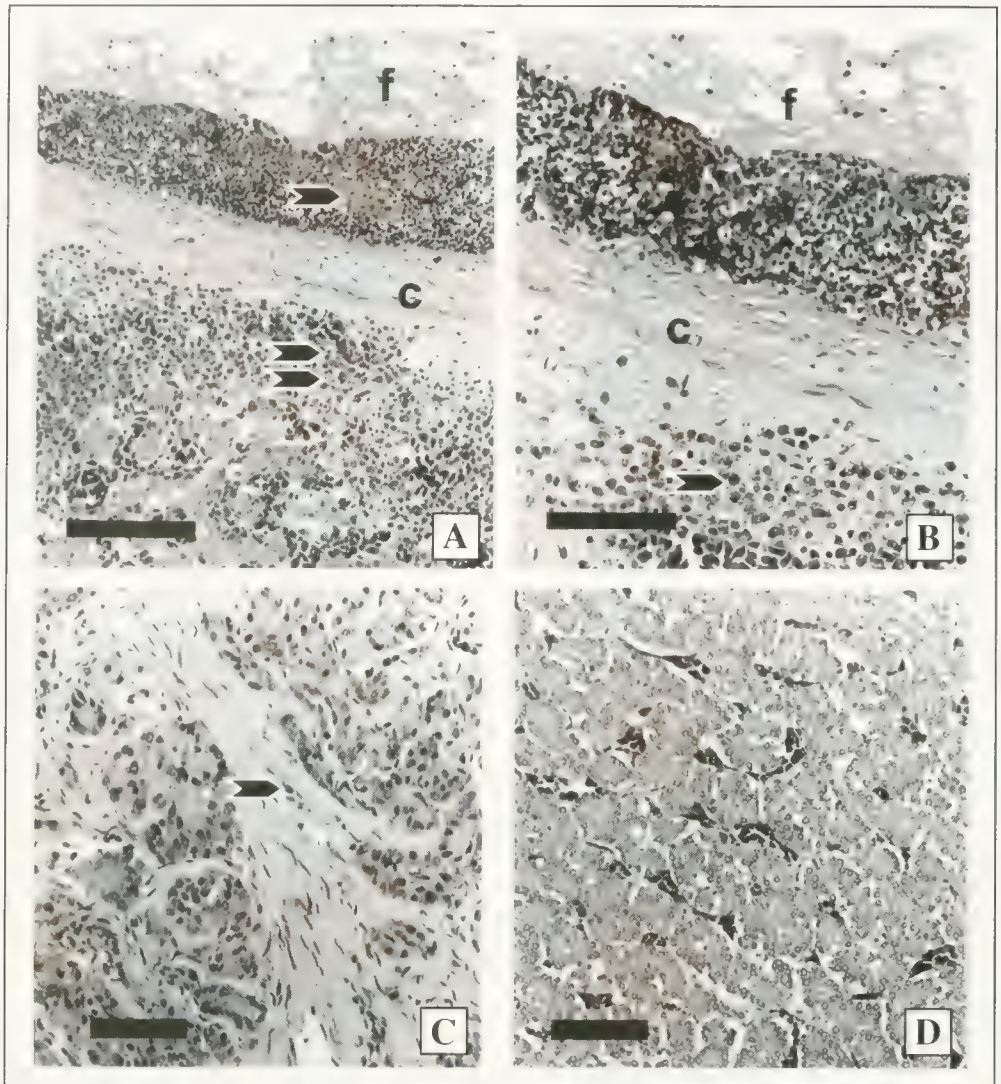

Figure 1

(**A**) Liver: Note fibrin (f), necrotic debris (large arrow), capsule (c), and inflammatory cells (double arrow), bar=100 µm; (**B**) Liver: note granulocytes (arrow), capsule (c), necrotic debris and fibrin (f), bar=50 µm; (**C**) Pancreas: Note large fibrous trabeculae coursing through pancreatic cells (arrow), bar=100 µm; (**D**) Normal pancreas from leatherback for comparison, bar=100 µm.

1:1 although slightly skewed towards females. Given the small sample size for each species, interpretation of the significance of the skewed sex ratio in our sample is problematic. Ross (1984) noted that bias in sampling, segregation of sexes in different areas, and small sample size could be responsible for deviations from the expected sex ratio of 1:1 in sea turtles.

Whether severe lesions of the digestive system occur commonly in leatherback sea turtles remains to be determined. Various factors can cause acute inflammation in the liver, including viruses, bacteria, protozoa, and poisons (Kelly, 1993); however, we saw no evidence of infectious agents in our histological examinations. Pancreatic fibrosis is a chronic lesion indicating earlier insult to the organ, secondary to infectious, toxic, or metabolic processes (Jubb, 1993). Necropsies of stranded leatherback sea turtles have revealed bacterial (Obendorf et al., 1987) and parasitic (Threlfall, 1979) infections, degenerative joint disease (Ogden et al., 1981), and struvite fecoliths (Davenport et al., 1993). The impact of these conditions to leatherback populations is unknown. Given the endangered status of East Pacific leatherback sea turtles, efforts to systematically evaluate health of these animals seem justified, including performing systematic necropsies on fresh carcasses recovered at sea or from nesting beaches, as well as performing health assessments of live animals on nesting beaches.

Lesions in the other species of sea turtles (olive ridley and green) were either mild, nonspecific, or absent al-

together. The absence of lesions in pelagic green turtles was in contrast to what is seen in immature and adult specimens caught in nearshore habitats. In those cases, most green turtles have systemic infections with vascular flukes or fibropapillomas (Aguirre et al., 1998). This would support the hypothesis that at least for immature turtles, these diseases, while absent pelagically, are acquired once the animals enter their near shore foraging pastures. It is possible that very mild subtle lesions could have been overlooked because many tissues had freeze-thaw artifacts. Should this be a major concern, future studies may focus on doing necropsies on freshly dead turtles caught on fishing boats; however, the logistics of doing this will be more complicated. For example, vessels of the Hawaii-based longline fishery are at sea for weeks at a time fishing many hundreds of km from port.

Stomach contents of olive ridley sea turtles in this study (pelagic snails, pyrosomas, foreign bodies) were similar to those seen by others (Parker et al., 2002; National Marine Fisheries Service and US Fish and Wildlife Service[3]). The presence of multiple baits in some olive ridley sea turtles suggests that animals may graze from longline hooks. Pyrosomas are found in stomachs of leatherback and green turtles (National Marine Fisheries Service and US Fish and Wildlife Service[4,5]), and leatherbacks are also attracted to hooks baited with sama (Grant[6]) and squid (Skillman and Balazs, 1992). Given that fisheries may play a significant role in the decline of leatherback sea turtles (National Marine Fisheries Service and US Fish and Wildlife Service[4]), determining whether bait attraction or entanglement pose the greater threat may be of management value. Similarly, evaluating the basis of bait attraction for olive ridley sea turtles caught in longline fisheries may provide clues that will help discourage interactions between this species and fisheries.

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Preparation of papers

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